BOTANY

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Volume LXXXII Number 1

The BOTANICAL GAZETTE

FOUNDED BY JOHN M. COULTER

SEPTEMBER 1926

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Volume LXXXII Number 1

THE BOTANICAL GAZETTE

A JOURNAL EMBRACING ALL DEPARTMENTS OF BOTANICAL SCIENCE

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For September and October, 1926

Brains of Rats and Men

That man's brain has been slowly developed from other kinds of animal brain structures, that human behavior patterns and the noblest human faculties are functions of man's peculiar protoplasmic organization—to many these still seem difficult statements to accept. Their truth, however, is further demonstrated by C. Judson Herrick in *Brains of Rats and Men*, his new book on the origin and biological significance of the cerebral cortex. It is a volume that belongs to that rare class of scientific works of genuine literary merit, in which Mr. Herrick traces the evolution of this amazingly complex organ from fishes to men, and follows step by step the elaboration of its functions.

Objective behavior and subjective experience are here reformulated in biological terms. Mr. Herrick demonstrates incisively that the entire intellectual, emotional, and moral life of mankind can be explored as biological functions without loss of their supreme values as distinctively human attributes and without passing outside the realm of natural laws.

Others have tried to read human faculties backward into the lower animals. Mr. Herrick reverses the order and, beginning with the simplest structures prophetic of cerebral cortex, he reads this history through to its culmination in man. He outlines also the development of the thalamus and corpus striatum and their functional relations with the cortex.

He turns then to the mechanism of learning, centering the discussion about the brains of rats and men, the two species of mammals whose behavior patterns have been studied most intensively under conditions of laboratory control. Recent experiments upon learning in rats are summarized.

In considering the transition from brute to man, Mr. Herrick calls attention to the fact that the brain of man is more than twice as heavy as that of an ape of equal body weight and that this increase is chiefly in the cerebral cortex. The complexity of the internal texture of the human cortex surpasses that of an ape in still larger measure.

Mr. Herrick emphasizes the unscientific character of the oversimplification of human behavior so popular in some psychological circles. He believes that human nature cannot be understood without recognizing that its patterns of behavior are very different from those of rats and monkeys, and that conscious experience is an essential component of these human behavior patterns in their biological aspects.

Approaching the problems of human nature from the biological side and with biological technique, the author works out a common ground upon which objective psychology and introspective psychology may meet without sacrificing what is good in either method. He has demonstrated that, without transgressing the boundaries of biological science, we can set in their places objective behavior in all its manifestations: affect, impulse, volition, and the whole intellectual and moral life together with the structural mechanisms employed.

The concluding chapters have a special significance for psychology and education, since they throw light upon such problems as the subconscious, complexes, habit, vital reserves, experience, association, will, and the relations of mind and body.

This account of the cerebral cortex, its evolution and its functions, by one of America's foremost neurologists touches upon problems that are fundamental to all the sciences that take living things, and man in particular, as their province: biology, psychology, anthropology, the social sciences, education, medicine. *BRAINS OF RATS AND MEN.* By C. JUDSON HERRICK. *$3.00, postpaid $3.15.*

* * *

"Liberty, Equality, Fraternity"

Beyond all other ideas of government, democracy means not merely a governmental mechanism, but a way of life. The social philosopher who thus broadly conceives it must turn to the most general interests of mankind. Thomas Vernor Smith, in his new book *The Democratic Way of Life*, re-endows "Liberty, Equality, Fraternity"—worn slogans of a goal that has never been reached—with some of the spirit of the days when they were magic words; and makes a brilliant commentary upon the questions of humanizing work, the proper use of leisure, religion in a democracy, birth control, and democratic leadership.

To make clear the abiding real content of the democratic trinity of ideals, Mr. Smith inquires into these goals as they stand today. He looks upon liberty as fundamental, a natural end for life, and would restrict it only for the sake of fraternity. He admits that liberty is neither more nor less than doing as one pleases, but believes that through proper education men may please more and more to act fraternally.

Fraternity, Mr. Smith holds to be a natural and ethical end for man. It is, in his view, the basis of religion, and the function of religion in a democracy is to foster brotherhood within the group and universal brotherhood.

What can equality as an ideal mean in the light of the present-day facts? Mr. Smith's equalitarian ideal means fundamentally that whatever objects or activities are regarded as good must be admitted to be as good when experienced by one person as when experienced by another. He sees in war and industrial autocracy the archenemies of equality, and in the cessation of wholesale hostility, the development of industrial democracy, necessary measures for the attainment of the equality ideal.

Bertrand Russell has expressed the belief that with present technology, the four-hour day awaits only the will to have it. Regarding such optimism as at best prophetic of a distant time, Mr. Smith, in considering work and leisure, prefers to place emphasis upon the humanizing of work, and to give up the tenaciously held idea that the good life is to be found exclusively in leisure. The supreme moral task of the hour, in Mr. Smith's view, is in banishing drudgery and monotony, and investing otherwise unpleasant work with meaning.

What kind of leadership is needed in a democracy? Mr. Smith rejects the conception of leadership of prestige and authority inherited from monarchies, and replaces it with the new conception of leadership suggested by science. The new type of leader is a leader by virtue of knowledge, and his function is to point, not to order. Science having discredited the spectacular and omniscient type of leader, democracy must be judged not by its ability to produce a few "master-leaders," but by its ability to make every citizen a creative leader in some enterprise.

Mr. Smith has brought to these principles of democracy, upon which so much enthusiasm has been lavished and over which so much disappointment has been felt, an undeniable tinge of modernity. He has formulated a democratic credo, a profession of the social faith of a modern man. *THE DEMOCRATIC WAY OF LIFE.* By THOMAS VERNOR SMITH. *$1.75, postpaid $1.85.*

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The new *Introduction to the Study of French* by Otto F. Bond will make a place for itself among French texts where the rapid attainment of the ability to read and understand French is the end most desired. Teachers who find that the prolonged syntactical study and delayed actual reading made necessary by most grammars is somewhat boring both to instructor and student will welcome this grammar which equips the student in twenty lessons to read interesting material.

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In an article in the *Modern Language Journal* for April, 1926, Mr. Bond says: "If Mary White wants to read *Le Petit Chose* or *Abeille* before she can order from a French menu or juggle a pair of partitive constructions in a negative sentence, why not let her do it? She cannot fail to get some good out of the performance even if she doesn't get all the story with full literary appreciation. Suppression of her desire to read cannot be expected to heighten her interest in partitive constructions!"

In preparing a text which concentrates on the problem of getting the student to the point where he can follow his natural interest in reading, Mr. Bond has performed a valuable service for instructors whether or not they agree with him that the primary aim of the junior college course should be the development of reading ability. The text may be followed by the direct method or the grammar-translation method, and its value as a starting-point for the course and a means for creating interest in the course is not lessened.

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VOLUME LXXXII NUMBER 1

THE
BOTANICAL GAZETTE

September 1926

VASCULAR ANATOMY OF RANALIAN FLOWERS[1]

I. RANUNCULACEAE

GEORGE HUME SMITH

(WITH THIRTY-FOUR FIGURES)

The origin of the angiosperms has long been a question of debate among botanists. One of the chief topics of controversy in this debate has been the nature of the primitive angiospermous flower. To many the external appearance of the Ranalian flower suggests that it is of simple and primitive construction; but, because facts hidden to the student of external morphology and anatomy frequently appear when the internal anatomy is studied, the present investigation was undertaken to determine the exact nature of the vascular anatomy of the Ranalian flower. Members of eight prominent families (Ranunculaceae, Menispermaceae, Calycanthaceae, Anonaceae, Magnoliaceae, Lauraceae, Berberidaceae, and Nymphaeaceae) were selected for study. As the investigation progressed it was discovered that the order consists of several more or less unrelated groups. The groups are: (1) Ranunculaceae, Menispermaceae, and possibly Calycanthaceae; (2) Lauraceae (probably closely related to 1); (3) Berberidaceae; (4) Nymphaeaceae; (5) Anonaceae; (6) Magnoliaceae. Of these five or six groups, the vascular anatomy of the Ranunculaceae is clearly the most simple and least specialized. The present report, therefore, confines itself entirely to a description and discussion of the vascular skeleton of the flowers of typical mem-

[1] Presented to the Faculty of the Graduate School of Cornell University in partial fulfillment of the requirement for the degree of Doctor of Philosophy.

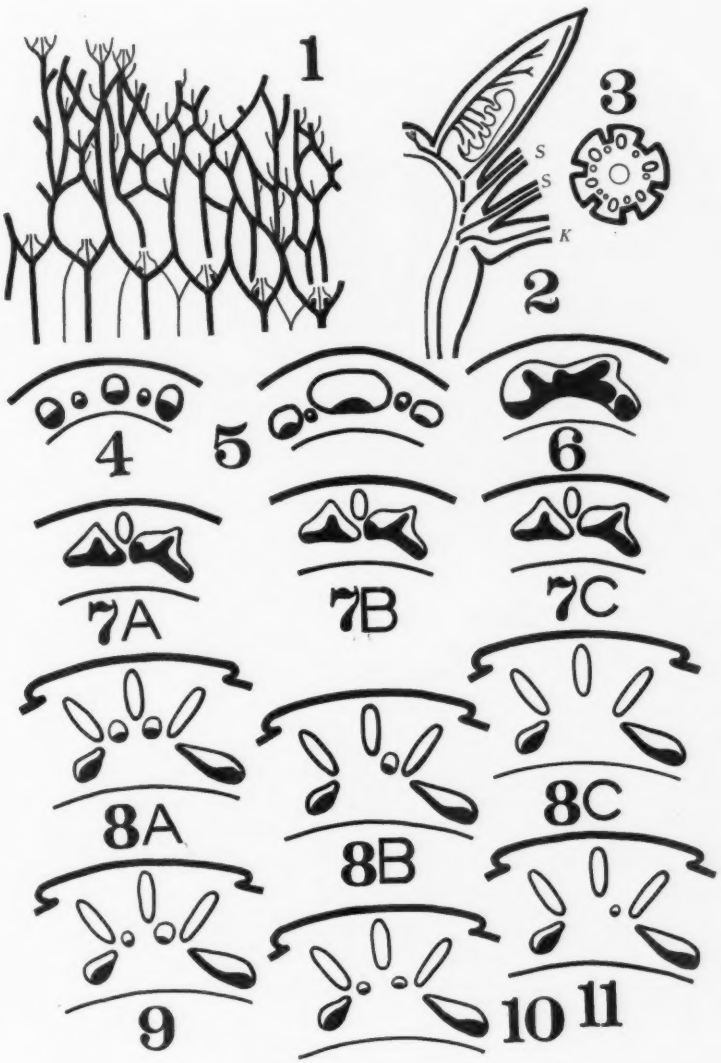
bers of the Ranunculaceae. Subsequent papers will consider the remaining families.

The members of the Ranunculaceae studied are *Caltha palustris* L., *Trollius laxus* Salisb., *Coptis trifolia* (L.) Salisb., *Actaea alba* (L.) Mill., *Actaea rubra* (Ait.) Willd., *Hepatica triloba* Chaix., *Hepatica acutiloba* DC., *Anemone quinquefolia* L., *A. canadensis* L., *Clematis virginiana* L., *Isopyrum biternatum* (Raf.) T. and G., *Anemonella thalictroides* (L.) Spach., *Thalictrum dioicum* L., *Ranunculus hispidus* Michx., *R. abortivus* L., *R. septentrionalis* Poir., and *Aquilegia canadensis* L.

Caltha palustris

ILLUSTRATIONS.—Fig. 1 is a diagram of the course of the vascular bundles upon the unrolled surface of a flower. It is an actual tracing from a single flower. The narrower lines represent the departing traces; the broader lines represent axial strands. The diagram maps completely all vascular tissue in the sepal region. The mapping is incomplete above this level, as the abrupt ending of some of the broader lines (axial strands) indicates. Several difficulties made it impossible to map these regions completely. Three of the carpels are shown in the upper lefthand portion of the figure. Fig. 2 is a median longitudinal section of a flower drawn with the aid of a camera lucida. Fig. 3 is a cross-section of a pedicel. Figs. 4–11 are cross-sections of segments of the receptacle in the region of sepal trace formation, and are drawn with the aid of a camera lucida. Figs. 4, 5, 6, 7*a*, 8*a* are successive levels of one segment. Figs. 8*a*, 9, 10, 11, and 8*c* illustrate the derivation of the unilacunar sepal supply from the trilacunar.

DESCRIPTION.—In the peduncle of the flower the vascular tissue is arranged in the form of a hollow cylinder composed of 10–20 separate strands (figs. 1, 3). These strands are of two sizes, large and small. The smaller are intercalated between the larger singly or in pairs. As the slender peduncle gradually swells into the bulbose receptacle (figs. 2, 3–5), the cylinder of vascular tissue increases in diameter proportionately. Coincident with the outward, upward movement of the strands, each large strand gradually becomes broader in the tangential direction, so that the vascular tissue more nearly approaches a continuous ring of tissue. Then each of the



FIGS. 1–11.—*Caltha palustris:* explanation in text

strands, in a definitely spiral succession, gives rise to the entire supply to the sepal facing it (fig. 1). Almost invariably this supply consists of three traces. In the formation of these three traces, the large and tangentially elongated strand facing the sepal divides radially into three (figs. 6, 7). The median one of these three strands departs directly outward and upward through the receptacle into the median portion of the sepal as the median trace to the sepal. Its departure initiates the median sepal trace gap. The two lateral strands remain a portion of the cylinder. Within a distance of less than 10 μ a projection appears on each of these axial strands (fig. 7*a*, *b*, or *c*). Soon these projections become differentiated into distinct strands (fig. 8*a*, *b*, or *c*). These pass outward and upward as the right lateral and the left lateral traces to the sepal.

As figs. 7 and 8 illustrate, the point of origin of the projections determines the number of separate gaps formed. Thus, in the departure of the three traces to a sepal, one, two, or three separate and distinct gaps in the axial vascular tissue result; and the number of axial vascular strands is two, three, or four. Of these axial strands the two outermost are always large and well developed; the inner ones, when present, may be large and strongly developed, or any size of a grading series until completely absent (figs. 8–11).

In the foregoing statement it has been mentioned that the number of traces to a sepal is three. Occasionally the uppermost and smallest sepal of the series appears to receive but a single strand. Such an illustration would be similar to fig. 8*c*, with the two lateral traces omitted and the base of the sepal somewhat more constricted.

Above the sepal level the axial cylinder shows the following facts. The number of axial strands has been more than doubled by the departure of the sepal traces, and each small pedicel strand has fused or is fusing with its larger axial neighbor. From this circle of strands the first stamen trace arises by the dissection of an axial strand. This dissection occurs at a point almost directly above the position of the first sepal, and at a level slightly higher than that of the last sepal (fig. 1). Similarly the traces to the other stamens appear in a rapid and more or less spiral succession. In the dissection of an axial strand to form a stamen trace, the axial strand splits radially into either two or three parts. If the division is into two parts, one strand remains axial and the other departs outward as

the entire supply to the stamen facing it. If the division is into three parts, the median one of these becomes the supply to the stamen and the two lateral strands remain axial. Whenever this "tri-section" of an axial strand occurs, the number of axial strands is increased. This increase in number of axial strands is counterbalanced by an equally frequent fusion of adjacent axial strands. This constant union of axial strands and subsequent division to form new axial strands and traces is repeated without interruption until the termination of the axis is reached; hence a netlike appearance to the cylinder results.

Following the departure of the trace to the last stamen, the vascular supply to the first carpel arises. The supplies to the other 3–12 or more carpels arise in a rapid spiral succession. The supply to each carpel consists of three separate traces. Each trace originates directly from the axial cylinder. In the supply to the individual carpel the dorsal trace arises first. An axial bundle segments radially into three strands. The median of these departs from the axis and passes up the dorsal margin of the carpel. At a point on the axial cylinder very slightly above the point of departure of the dorsal trace, each of the two axial strands which have resulted from the departure of the dorsal carpel trace divides radially into two strands. Of these the one nearer the dorsal trace gap becomes a ventral trace. Some axial strands definitely and abruptly terminate with the departure of the last carpel trace arising from that particular strand, but the majority do not. The axial strand continues upward, but quickly frays and rapidly fades away within a distance of 10–20 μ. In fraying, the few spiral elements wander toward the tip of the cone-like receptacle (figs. 1, 2).

Within the carpel the three traces act in a very characteristic manner (figs. 2, 28). The dorsal trace passes unbranched up the dorsal margin of the carpel and fades as the stigma is approached. The two ventral traces pass up along the ventral suture and fade away within the stylar region. In the lower portion of its course, each ventral trace gives off inwardly a series of strands to the number of about ten. Each of these strands enters one ovule of the row of ovules situated directly under this trace.

Discussion.—Three important features of the axial skeleton as a whole are to be noted. (1) The skeleton appears as a hollow cylindrical network of strands bristling with departing traces. Thus it

discloses a similarity to the vascular design of a vegetative axis. (2) The spiral insertion of the floral organs upon the axis emphasizes the similarity between vegetative and floral axes. (3) The fact that each trace to each organ emerges from the cylinder and passes directly outward and unbranched to the organ, designates the floral axis as entirely primary. If the floral axis (receptacle) were an inflorescence, each floral trace would display some evidence of nodal differentiation.

The apical portion of the floral axis also deserves special consideration. The presence of remnants of vascular tissue above the level at which the last carpel trace has departed indicates that the most apical of the floral organs have entirely disappeared. The reasons for this conclusion are three. (1) Vascular tissue, historically, always terminates in some spot where it is physiologically valuable. (2) In the consideration of evolutionary series, it has been found that vascular tissue never arises in advance of the structure it is to supply. (3) The vascular tissue to an organ, on the other hand, may remain after the organ itself has disappeared. Thus *Caltha palustris* can be added to the list of those forms showing a suppression of floral organs.

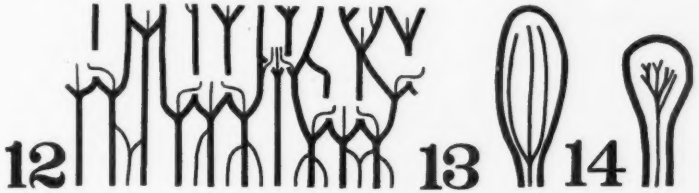
In the description of the sepals, it has been pointed out that many sepals receive three traces arising so that three separate gaps are formed, and that a grading series can be constructed from this type to one culminating in the departure of three traces from a common gap (figs. 8*a*, 9, 10, 11, 8*c* in the order named). The justification in reading the series in this direction lies in the fact that a general tendency exists among the angiosperms toward a reduction in the amount of woody tissue. Herbaceous forms, for instance, have been derived from woody forms.

The carpels are three trace multiovulate structures. As the discussion progresses and other carpellary conditions are described and explained, it will become apparent that this three trace multiovulate condition is primitive.

Trollius laxus

DESCRIPTION.—This flower is constructed upon the same general plan as *Caltha*. It differs in five respects. (1) Ten to twelve large strands and at least an equal number of smaller alternating strands

are present in the peduncle (fig. 12). (2) Each of the 4–15 sepals receives three traces. These traces are derived from the simultaneous division of three large axial strands after the manner shown in fig. 12. Note that three distinct gaps are always formed. (3) Above the sepals 15–25 small club-shaped "petals" are present. These are arranged spirally, receive one trace each, and this spiral merges into the spiral of the stamens. (4) Within the carpel, strands pass from the ventral traces to the ovules, one to the ovule; and, in addition, above the ovules strands pass inward from the ventral traces to the ovulary cavity and end abruptly (fig. 27). (5) No fraying of the termini of the axial strands of the receptacle or other evidence of the suppression of terminal carpels exists.



FIGS. 12–14.—Fig. 12, *Trollius laxus:* vascular system of axis of sepal and lower petal region of flower, split open and spread out in one plane; fig. 13, petal; fig. 14, *Coptis trifolia*, petal.

DISCUSSION.—***Trollius***, therefore, presents two new problems. One considers the evidence of the staminodal affinity of the petal; the other deals with the possibility of the presence of suppressed ovules.

The sepals and petals are clearly unlike in external appearance. The sepal is broad and expanded, and with an unconstricted base. The petal is small and inconspicuous, and the basal portion is slender and filamentous. In vascular anatomy these two organs also differ radically. The number of traces entering a sepal is three. Within the sepal these branch profusely and the sepal becomes thoroughly net-veined. A single trace enters the petal. It does not branch until it enters the expanded portion, and then it subdivides into three prongs, which extend parallel and unbranched to the apex of the organ (fig. 13).

On the other hand, the petal resembles the stamen in several respects. The club-shaped appearance with the long and slender filamentous basal portion makes the resemblance to stamens noticeable. Again, the vascular anatomy is indistinguishable from that of the stamen, not only because both are organs receiving a single trace, but also because the first stamen trace departs from the axis immediately after the last petal trace and in direct continuation of the spiral order. Thus external similarity and internal anatomy identify the petal with the stamen.

The behavior of the vascular tissue within the carpel gives ample evidence that the carpel of *Trollius* has been derived from a form having a larger number of ovules. As fig. 27 illustrates, a series of strands is given off from each ventral trace toward the ovular cavity. The lower of these enter ovules, but the upper ones end abruptly at the margin of the cavity. Thus the form, course, and position of these traces suggest that they are supplies to suppressed ovules. Again, if these strands are not traces to ovules, what can be the original physiological significance of their presence? What tissue could they have been intended to supply? They cannot be the forerunner of an increase in the number of ovules of the carpel, because vascular tissue has never been known to appear as a forerunner to the evolution of an organ. On the other hand, vascular strands may remain lagging behind after the organ has disappeared; therefore the anatomical evidence points to the conclusion that these traces are supplies to suppressed ovules.

The theory that these traces are supplies to suppressed ovules gains additional support from other morphological data concerning Ranunculaceae. ERNST BESSEY (7) discovered one or more rudimentary ovules present above the functional ovule in *Anemone caroliniana* Walt., *A. canadensis* L., and *Pulsatilla hirsutissima* (Pursh.) Britt. In some cases these ovules were represented only by a few-celled rudimentary archesporium, the presence of which would not have been discernible to one not studying the comparative development of pistils. Again, GUIGNARD (10), in his investigations of the embryo sacs of angiosperms, figures a specimen of *Clematis cirrhosa* showing one fully developed ovule, and above it two partially de-

veloped ovules. BAILLON (2), in his discussion of the Ranunculaceae, found accessory ovules so common in *Anemone* that he concluded that the number was actually five, but four had degenerated and the fifth, at the expense of the others, remained. From the standpoint of systematic evidence, C. E. BESSEY (6) argued and proved the dictum "uniovulate from multiovulate." Thus the vascular anatomy of the pistil of *Trollius laxus* confirms and strengthens the contention that the evolutionary tendency has been toward a gradual reduction in the number of ovules contained in a pistil.

Coptis trifolia

DESCRIPTION.—*Coptis* differs anatomically from *Trollius* in but seven minor respects. (1) The peduncle contains only about seven vascular strands; usually five are large, and the remaining smaller and either lignified or unlignified. (2) In sepal trace formation the broadened axial strands split radially into two to six strands. (3) The divisions of these strands are such that each sepal receives three traces, and the number of axial bundles is increased to above ten. (4) The divisions are so rapid that no definitely spiral order can be discerned. On the other hand, the arrangement is not clearly cyclic. (5) Above the sepal level the axial bundles are not clearly set apart from each other, because the stamen traces depart in very rapid succession and the gaps are quickly closed. (6) Within the carpel the ventral traces give rise to no strands which do not supply ovules. Thus the ventral traces do not show evidence of supplies to suppressed ovules. (7) The trace entering the "petal" gives rise to several small lateral branches in the more expanded bladelike portion (fig. 14). Fundamentally, however, the "petals" are merely modified stamens as in *Trollius*.

Actaea

DESCRIPTION.—In *Actaea alba* the vascular anatomy of the flower up through the stamen level is very similar to that of the preceding genera. A cylinder of strands variable both in number and in size enters the receptacle. At the first division of these strands the sepals are supplied with three traces each. These traces arise as

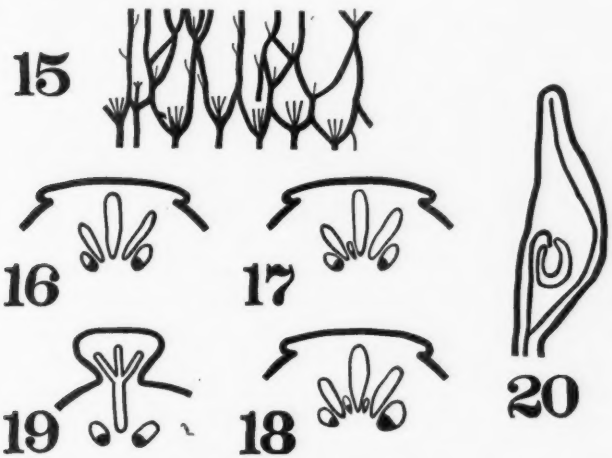
three radiating fingers from a common gap. The traces to the petals and the stamens are one each. Consequently the petals are indistinguishable from the stamens, so far as the vascular supply is concerned. Above the stamen level certain interesting differences occur. After the last stamen trace has departed, the five or six axial strands rapidly coalesce into three. These three strands continue up the axis in this formation to the base of the single carpel. Within the carpel the median of the three strands becomes the dorsal trace; the two lateral ones become the ventral traces. The dorsal trace passes up the dorsal margin of the carpel, and early in its course gives rise to a few fine lateral branches, but itself remains strong to the stigmatic region. The two ventral traces give rise to occasional branches which ramify the marginal tissue toward the dorsal portion of the carpel. At the same time they give off inwardly individual branches to the two rows of ovules.

DISCUSSION.—The vascular plan of the receptacle above the stamen level raises three questions. (1) Does the interval between the last stamen and the pistil represent a single elongated internode, or does it represent the pistillate portion of the receptacle with all pistils suppressed but one? The vascular cylinder of this region gives off no blind traces, therefore the presence of intervening pistils cannot be assumed. On the other hand, not only the intervening pistils but also the evidence of vascular supplies to them may have disappeared. (2) Is the pistil terminal? If it were pseudo-terminal, the ends of the axial vascular strands of the receptacle would probably show frayed projections beyond the departure of the pistil supply such as *Caltha* displays. (3) Is the pistil a single carpel? The number of strands entering the base of the pistil is three. Of these two are ovule-bearing (ventral) and one is dorsal. This fact (three strands) makes it a simple pistil, because throughout all of this investigation of the Ranales and all records mentioning the number of traces entering the angiospermous carpel the number is three, or a modification of this number. A pistil, if compound, will show anatomical evidence of receiving more than one dorsal and two ventral traces. The truth of this statement will be expanded in the consideration of the Berberidaceae.

In *Actaea rubra* the floral anatomy is precisely that of *A. alba*.

Hepatica

DESCRIPTION.—In *Hepatica triloba* the course of the 10–12 strands through the peduncle and the receptacle (fig. 15) is very similar to that of *Caltha*, except that the bundles are not all of uniform size. At least 6–9 are large and strongly lignified; the remainder are smaller. Some or all of these smaller strands are unlignified. These smaller strands join their larger axial neighbors at about the level of sepal trace formation, or completely fade away at about this level.



FIGS. 15–20.—*Hepatica triloba:* fig. 15, diagram of vascular system of axis of sepal and lower stamen region of flower spread out in one plane; figs. 16–19, cross-sections to show modes of lateral sepal trace departure; fig. 20, carpel.

In sepal trace formation the large axial strand facing a sepal elongates tangentially and splits radially into 3–7 strands. Commonly the segmentation is into five strands. The median three of these strands depart simultaneously from the cylinder as three spreading fingers, and enter the sepal as the three traces to the sepal (fig. 16); thus but one gap is formed. Occasionally an axial strand divides into six strands instead of five. As a result, one lateral sepal trace and the median sepal trace enjoy a common gap, whereas the other lateral trace enjoys a distinctly individual gap (fig. 17). This

distinctly individual gap may or may not be quickly closed by the union of the two adjacent axial strands. Even less frequent is the segmentation of the axial strand into seven. The two lateral sepal trace gaps are thus separated from the median sepal trace gap by axial vascular tissue (fig. 18). Another variation frequently occurs whenever the number of sepals is over five or six. The smaller and higher sepals receive but a single trace. In the derivation of the supply to such sepals, the tangentially expanded axial bundle facing the sepal divides into three parts; the two lateral remain axial, the median passes into the sepal as an undivided unit. Immediately upon entering the sepal, a subdivision of this unit into three strands occurs (fig. 19).

The first traces arising above the sepal level pass to the stamens, one to each stamen. After the stamens are supplied, the traces which arise from the axial framework pass to the carpels, one to each carpel. The axial strands terminate as traces to carpels. That a single strand enters a carpel, instead of three, is an important distinction between this genus and the foregoing genera.

Within the carpel the course of the vascular strand (figs. 20, 33) differs from that of *Caltha*. In the base of the carpel the strand splits into two portions. One follows the dorsal margin to the stigma, the other proceeds directly up into the single ovule.

The vascular anatomy of the flower of *Hepatica acutiloba* is identical with that of *H. triloba*.

Discussion.—As in *Caltha*, the behavior of the vascular strands at the level of sepal trace formation again gives evidence that the three trace, single gap condition is derived from a three trace, three gap condition (compare figs. 16–18 with figs. 8*a*, *b*, and *c*).

Consider now the higher smaller sepal which frequently receives but a single strand. Because the majority of *Hepatica* sepals receive three traces arising from a common point (fig. 16), the definitely three prong division of the single strand, such as enters the type of sepal under consideration (fig. 19), suggests an unusually close adherence of the lateral traces to the median. Thus in *Hepatica* a second tendency of sepal traces is manifest, namely, lateral fusion of adjacent traces to form a single strand.

The carpel receives but a single vascular strand and contains but

a single ovule. The full significance of the fact that a carpel receives but one trace and contains but one ovule cannot be appreciated until the carpels of *Ranunculus*, *Aquilegia*, and *Calycanthus* have been considered. A discussion, therefore, of the origin of the single trace, uniovulate carpel is deferred.

Anemone

In all essential respects *A. quinquefolia* and *A. canadensis*, both studied by the writer, and *A. coronaria* studied by HENSLOW (12) are of the same fundamental design as *Hepatica*. Likewise, *Isopyrum biternatum* is very similarly constructed.

Clematis

In *C. virginiana* each sepal receives three or four traces. Each of these traces arises from a separate point on the vascular cylinder and leaves a separate gap. This is the most striking and only difference of importance from *Hepatica triloba*. HENSLOW'S (12) description of *Clematis vitalba* L. shows that it differs from *H. triloba* in a similar respect. As *Clematis* is the only genus studied of this family in which the number of sepal traces is more than three, no direct corroborative anatomical evidence is at hand upon which to build any explanations for this condition.

Anemonella thalictroides and Thalictrum dioicum

DESCRIPTION OF ANEMONELLA.—In all respects not specifically mentioned, the design of the vascular framework of a flower of *Anemonella thalictroides* (fig. 21) is similar to *Hepatica*. The pedicel most frequently contains seven equal sized, equidistant vascular strands. In some cases this number increases to eight or nine in the base of the receptacle by the radial division of one or two of the strands. The subdivision of the axial vascular strands during the process of sepal trace formation displays a greater variation than in the genera previously described. A strand splits radially into 2–5 strands, 1–3 of these departing from the cylinder as sepal traces. The other remains axial. Most sepals receive three traces, although two trace sepals are not infrequent. The three traces to a sepal may arise from one, two, or three separate and distinct axial strands. The number of distinct

gaps formed by the passage of traces to a sepal is 1–3, according to the mode of origin of the individual traces (fig. 21). The strands which remain axial give rise to the stamen and the carpel traces.

FIGS. 21–23.—Fig. 21, *Anemonella thalictroides:* diagram of vascular system of axis of sepal region of flower spread out in one plane; figs. 22, 23, *Thalictrum dioicum:* similar diagrams of staminate and pistillate flowers respectively.

Within the basal portion of the carpel the trace branches into a dorsal and a ventral strand, as in *Hepatica*, but each of these in turn subdivides until every rib of the carpel is supplied with a vein. The carpel of *Anemonella* is 8–10-ribbed. Of the veins of ventral origin, the largest and most prominent forks into three strands after it has traversed about two-thirds the length of the carpel wall. Of these three strands the two lateral ones continue up the carpel wall to the style and fade away; the median one of the three curves inward and downward to the ovule.

DESCRIPTION OF THALICTRUM DIOICUM.—In the staminate flower of *T. dioicum* (fig. 22) the pedicel contains about eight vascular strands. As they approach the level of sepal trace formation, each strand expands tangentially and splits radially into 2–5 strands. Some of these are sepal traces and each of the 4–5 sepals receives 1–3 traces. Eight to sixteen strands remain axial after the sepals are supplied. These quickly divide into a number of strands equal to the number of stamens, and a strand enters a stamen as the total supply to that stamen. The vascular anatomy gives no hint of a terminal carpellary region.

The plan of the vascular skeleton of the carpellate flower of *T. dioicum* (fig. 23) is practically the same as that of the staminate flower. The axial strands in the pedicel and lower receptacle are usually four. These split into a variable number of strands. Of the

resulting strands, some pass to the sepals, 1–3 to the individual sepal, and the others remain axial. After sepal trace formation, the axial strands, with the possibility of an occasional union of two adjacent strands, quickly separate into a number of traces equal to the number of carpels (about 9). Within the carpel (fig. 34) the trace divides into two strands; one bears toward the dorsal side of the carpel and the other to the ventral. These extend upward along diametrically opposite ribs of the carpel. As soon as the dorsal and ventral strands have become differentiated, each of them gives off lateral branches. Some of these in turn subdivide until every rib of the carpel has received a vein. At a still higher level the ventral strand proper gives rise to another branch. This curves inward and downward to the ovule. Near the base of the style the two rib branches nearest the ventral strand proper reunite with it, and this vein extends upward to the stigmatic region. The remaining rib branches derived from the ventral strand and the majority of those of dorsal origin fade away at the base of the style. The dorsal strand proper and a certain few of its derivatives reach the stigmatic region.

Discussion.—In the sepal receiving three traces, the one is median and the others lie, one on the right side and one on the left side of the median trace; whereas in the sepal receiving two traces, one trace occupies the median position, the other that of one of the lateral traces, and a distinct vacancy occurs on the other side where another lateral trace could occur. Furthermore, within the sepal the first branch of the median trace assumes the burden of this missing lateral trace. Thus it is clearly evident from the anatomical facts as stated that the basic plan is three traces to the sepal in *Anemonella* and *Thalictrum*.

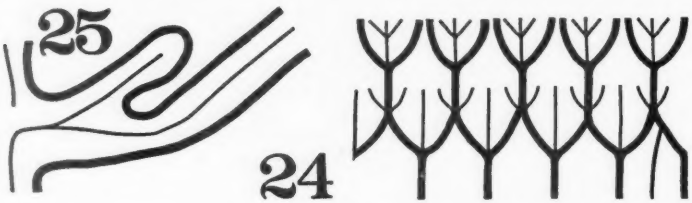
The carpels of *Thalictrum* (and *Anemonella*) receive but a single strand and contain but one ovule. In this respect these forms are similar to *Hepatica*. The branching, however, in each is more extensive than in *Hepatica*, and the ovule is not so nearly basal.

Thalictrum dioicum is the only species of the Ranunculaceae studied in which the flowers are both structurally and functionally imperfect. The anatomy discloses no conclusive evidence that the flowers were once perfect. In the staminate flowers, for instance, the terminal portion of the axial cylinder gives no indication of the abor-

tion of a terminal carpellary region such as the carpellary region of *Caltha palustris* might lead one to anticipate. The pistillate flower also gives no indication of a suppression of a staminate interval.

Ranunculus

DESCRIPTION.—In *R. hispidus* the number of vascular strands of the peduncle is either six or seven. Five of these are large, distinctly lignified, and equidistant from one another. The five sepals are directly above them. One or two smaller, yet distinctly lignified strands are also included in this circle in such a manner as always to be separated from each other by at least one large strand. As the sepal level is approached, each of the five large bundles splits radi-



FIGS. 24, 25.—*Ranunculus:* diagram of strands of vascular system of axis of sepal and petal region of flower; fig. 25, petal and attached nectariferous scale (*R. septentrionalis*).

ally into three (fig. 24). The median one of the three thus formed advances outward and upward through the receptacle, and becomes the median trace to the sepal facing it. By the departure of these five traces, the nearly complete cylinder of tissue is broken up into five groups of bundles. The members of a group converge and unite to form five bundles (fig. 24). Either just as this union into five bundles is occurring or just after it has been consummated, traces are given off from the vascular cylinder in such a manner that each sepal is supplied with a right and a left lateral trace (fig. 24). Note that the three traces to a sepal enjoy a common gap. At a slightly higher level the petals are supplied with one trace each (fig. 24).

As the petal trace passes outward through the parenchyma, which is transitional between the receptacle and the petal, it divides into three strands. These are the three primary veins of the petal, and

initiate its palmate venation. No vascular supply passes up into the small scale situated at the base of the petal. With the departure of the petal traces the number of axial strands is ten. These are equally distant and of uniform size. Immediately stamen traces begin to emerge from these axial strands after a fashion similar to that described for *Caltha*. It is also to be noted that the division of the axial strands is not simultaneous (cyclic) but spiral.

As in the preceding genera, the vascular cylinder of the floral axis becomes reticulate in appearance, due to the constant division and recombination of axial strands. With the departure of the last of the stamen traces, the axial strands arrange themselves into a more compact and less netlike cylinder, the gaps becoming fewer and less distinct. The sheathing parenchyma becomes very nearly a continuous enveloping ring. This condition continues through the short axial region which can externally be seen to separate the stamens and carpels. At the termination of this interval, the first carpel trace appears as a projection from the almost complete cylinder of vascular tissue. By the departure of the traces to the four or five following carpels, the vascular cylinder is dissected into numerous small axial strands, thus assuming again a distinctly reticulate appearance. From this type of axial cylinder the remaining carpel traces arise after a manner precisely analogous to that of the stamen region. One trace enters each carpel.

The course of the strand within the carpel is very definite (fig. 32). The single entering strand soon divides into two, one of which bears quickly to the dorsal side of the carpel, and extends upward and unbranched to the base of the stigma. This is the dorsal strand. The other (ventral strand) immediately forks into three portions, which advance directly upward, paralleling one another. At about one-fourth the length of the carpel wall, the median of these three strands turns abruptly inward and enters the ovule. A short distance above the ovular cavity each of the lateral strands sends a side branch through the carpel wall in the direction of the dorsal margin. Either or both of these side branches curve extensively enough to meet the dorsal strand. Sometimes the two lateral portions of the ventral strand end blindly at the base of the style; at

other times they come in contact with each other and then fuse with the dorsal strand; in still other carpels just one of the ventral strands fuses with the dorsal and the other ventral strand ends blindly.

Ranunculus abortivus differs from *R. hispidus* in just one respect, the two ventral strands of the carpel are merely two tiny stubs. As in *R. hispidus*, no vascular supply passes up into the small scale at the base of the petal.

The difference between *Ranunculus septentrionalis* and the other two species is due probably to the fact that the flower is considerably larger. Usually two, three, or even four small lignified bundles are present in the peduncle in addition to the five large strands. Again the lateral sepal traces are not given off as soon after the median sepal trace as in the other two species. It is also of interest to note that the first branch of the median vein of the petal arises from the ventral surface of the vein and passes up into the small scale situated at the base of the petal (fig. 25).

The vascular supply within the carpel is also slightly different from that of *R. hispidus*. The two ventral strands never branch extensively; usually just one of them gives rise to a branch which passes laterally.

In all three species studied occasional variations occur within the sepal region. An occasional sepal receives three traces, either arising so that three visible gaps are formed or only two. In this latter case the gap formed by the lateral trace alone is quickly closed by the reunion of the strands. In another type of variation, one or rarely both lateral traces are lacking.

Discussion.—From the data just presented, the sepals of *Ranunculus*, as those of *Caltha* and *Hepatica*, give evidence of an ancestry in which the three traces originally arose from three separate and distinct gaps.

The affinities of the petals are not easily seen. The petals of *Ranunculus* could be considered as sepals, with the three traces completely fused to the base of the organ; or the petals could be considered as sepals in which the two lateral traces have disappeared. While such possibilities of a relationship to sepals do exist, several facts point to the petal as an organ distinctly different from the sepal. The strongest evidence of a lack of relationship lies in the pres-

ence of the nectariferous scale at the base of every petal and its complete absence from every sepal. The fact that the nectariferous scales of two of the species studied receive no vascular supply suggests that the scale is an evagination of the petal itself. The fact that the vascular supply to the nectariferous scale of *R. septentrionalis* arises from a vein of the petal definitely confirms the conclusion that the nectariferous scale is not an independent organ secondarily fused with the petal, but actually is a part of the petal.

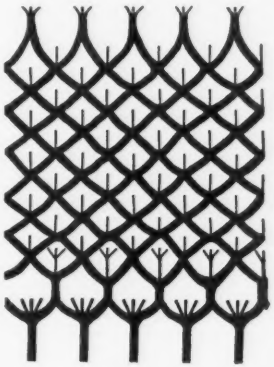


FIG. 26.—*Aquilegia canadensis:* diagram of strands upon unrolled surface of vascular system of axis of flower, split open and spread out in one plane.

Certain facts suggest the stamen affinity for the petal. The presence of but a single strand is one of these; but, as was pointed out, two other possibilities exist as to the nature of this single strand. Additional facts, however, strengthen the possibilities of the stamen affinity of the petal. Whereas the number of sepals is always five and whorled, the petals are occasionally more than five and spirally arranged. Furthermore, when the arrangement is spiral, it is continued by the stamens without the slightest break. Thus the arrangement of the petals in these instances suggests a stamen affinity.

Aquilegia canadensis

DESCRIPTION.—The number of large vascular strands in the peduncle is five. Sometimes one or two smaller strands are present. In the lower receptacle the five large strands simultaneously segment radially into five parts each. The median three of each group of five pass outward and upward through the receptacle as three diverging fingers, and enter the sepal facing as the three traces to that sepal. The adjacent derivatives of two contiguous axial large strands unite on radii alternate with those occupied by the large pedicel strands at the time of sepal trace formation (fig. 26). These five strands soon divide radially into three each. As in *Ranunculus his-*

pidus, the median strand of each group of three departs as the total supply to the petal facing it. As this trace passes through the transitional zone from receptacle to petal, it branches into three parts. These three parts are the three primary veins of the petal. After a fashion analogous to that whereby the petal traces were formed, traces to the alternating whorls of five stamens each are formed. The single trace entering the individual stamen never branches.

The ten axial strands resulting from the departure of the last whorl of stamen traces pass up the axis in pairs as distinct strands for an appreciable distance. Then the two members of a pair unite only to redivide at once into three strands each. The three strands compose the supply to the carpel facing. Thus each carpel receives three separate traces, which are distributed so that the two lateral strands are the ventral traces and the median one is the dorsal trace to the carpel. The branching of these strands within the carpel is practically the same as in any of the flowers of the Ranunculaceae in which the carpels are supplied with three traces (fig. 28). These genera are *Caltha*, *Trollius*, *Coptis*, and *Actaea*.

In one specimen examined an interesting variation occurs in the derivation of the carpel supply (fig. 31). The ten axial strands resulting from the formation of the traces to the last whorl of stamens do not remain as ten distinct strands, but coalesce to form a definite hollow cylinder before reaching the carpel level. At this point the cylinder breaks up into three distinct bundles, and each bundle enters one of the three carpels. This specimen has but three carpels. In the base of each carpel the trace divides into the usual dorsal and two ventral strands. Thus these particular three carpels display characteristics common to such forms as *Caltha* on the one hand, and *Ranunculus* on the other. The single entering trace and its subdivision into dorsal and ventral strands is similar to the conditions in the achene of *R. hispidus*, which receives but a single strand; the branching of each ventral trace to supply a row of ovules is like that of *C. palustris*.

DISCUSSION.—*Aquilegia* is the only genus studied in which the numerical plan is five throughout and all parts are inserted in whorls. To prove conclusively the derivation of the whorled condition from the spiral, anatomical evidence should reveal three distinct steps.

The first step is one in which the floral axis is greatly compressed. Accompanying this vertical compression of the axis the "phyllotaxy" becomes high. As the evidence of the other Ranunculaceae studied reveals, the "phyllotaxy" of the stamen-carpel region is always too high to determine satisfactorily, and thus suggests a marked vertical compression. The second step in the derivation of the whorled condition from the spiral involves a still more pronounced vertical compression of the axis and a dropping out of some of the organs. Thus the compression of the axis and the disappearance of segments of each cycle of the spiral would cause the remaining organs to appear as inserted essentially in whorls. It is upon the question of the disappearance of some of the floral organs, the most essential feature of this second step, that the anatomical evidence is entirely lacking. No blind traces leading off from the axial cylinder and suggesting a connection with suppressed sepals, stamens, or carpels, interspersed among the surviving ones have been found. It is to be recalled that ample evidence was found for the suppression of ovules (*Trollius laxus*), and of the terminal carpellary portion of the axis (*Caltha palustris*), and other investigators (**3, 4, 8, 16**) have found remnants of vascular tissue to suppressed perianths, stamens, and other floral structures. The third step in the possible derivation of the whorled condition from the spiral involves a still greater shortening of the internodes, so that the remaining floral organs come into exact whorls. In other words, certain internodes become so short as to come into coincidence. *Aquilegia* itself may be taken as an illustration of this condition. Thus, so far as the anatomical evidence itself is concerned, only the spiral and strictly whorled conditions exist in the Ranunculaceae. The high phyllotaxy and evident vertical compression of the axis, however, are sufficient to suggest that the intermediate condition just discussed has historically existed in the derivation of the strictly whorled condition of *Aquilegia* from the spiral condition of the more primitive Ranunculaceae.

The anatomical proof is also somewhat intangible concerning the possible derivation of the five to numerous arrangement of floral organs from the indefinite arrangement so common in the other genera. Certain interesting anatomical facts, however, exist in this connection. Although in no species studied does the number of

axial strands of the pedicel consistently equal the number of sepals, in *Coptis* and *Anemone* the number of large pedicel strands is usually five, in spite of the fact that the number of sepals may be greater or less than this; and, in *Ranunculus* and *Aquilegia*, the number of large pedicel bundles is always five. Therefore in view of the fact that the smaller intercalated bundles found in *Anemone* suggest and actually show evidence that they are vanishing, and in view of the fact that in the majority of families in which a definite numerical plan exists the number of bundles is in harmony with the number and arrangement of the floral parts, the inference is that a tendency exists among certain genera of Ranunculaceae toward a completely five to numerous plan.

Another point of interest is the consideration of the sepal. The three traces to a sepal depart from the common gap. In this respect they are identical with the supplies to the majority of the sepals of *Hepatica triloba* (fig. 16). The condition differs from that of *Hepatica*, however, in that the individual sepal always receives three traces, always arising from a common gap, and in that the number of sepals is always five and whorled. In these last two respects (five to numerous and whorled) the sepal condition is similar to that of *Ranunculus*. Thus the sepals display a combination of certain characteristics found in the *Hepatica* and the *Ranunculus* type of flower.

The supply to the petal is identical in appearance with that of the normal five petal flower of *Ranunculus*. The petals are probably stamen-like, therefore, for the same reason that the petals of *Ranunculus* are stamen-like. The innermost stamens are scalelike and are sometimes described as scales. They are nevertheless distinctly stamens; both the similarity of vascular anatomy and the presence of underdeveloped pollen sacs are proof of this.

The carpels are multiovulate and usually receive three traces. The conditions, therefore, are similar to those of *Caltha palustris*. In one specimen described, however, the vascular tissue entering a carpel is in the form of a single strand. The evidence is in favor of considering this a modification of the distinctly three trace condition in which the three strands are fused laterally up to the base of the carpel.

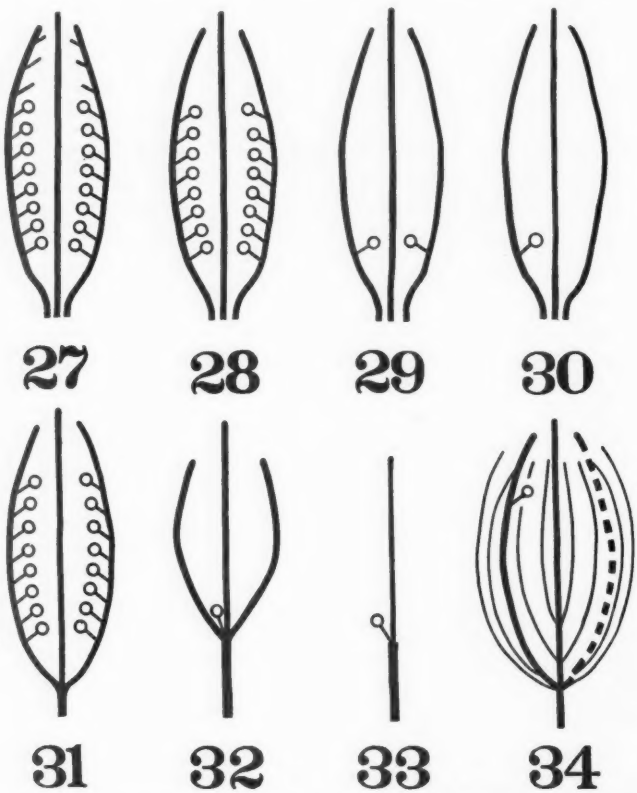
Conclusions

FLORAL AXIS.—The receptacle and pedicel, as a unit of structure, were considered in the discussion of *Caltha*. The description of each succeeding form has revealed similar characteristics. (1) The floral vascular skeleton is a pear-shaped network of strands studded with the departing traces. (2) Every trace passes directly and unbranched to an organ, thereby indicating that the axis is a simple flower and not a telescoped inflorescence. (3) The floral organs are generally inserted spirally. (4) The axis is divided vertically into three regions: carpel, stamen, sepal.

CARPEL.—In a general review let us first consider the vascular anatomy of the carpel of *Trollius laxus* (fig. 27). Three traces enter the carpel, a dorsal and two ventral. Each ventral trace supplies a row of ovules with one strand each, and gives off three or four additional strands above those to the ovules. These strands, according to the discussion of *Trollius*, are the supplies to completely suppressed ovules. If it is to be assumed that these strands themselves ultimately disappear, the resulting condition is portrayed by fig. 28. This figure also shows the vascular plan of the carpels of *Caltha*, *Coptis*, *Actaea*, and *Aquilegia*. Continuing the progressive suppression of ovules and subsequent disappearance of vascular strands, a condition is reached in which each ventral trace supplies but one ovule (fig. 29); and finally a condition is reached in which but one ventral trace supplies a single ovule (fig. 30). The two conditions just mentioned are actually found in *Calycanthus floridus* L. This species, as a future paper will discuss, is closely related to the Ranunculaceae. Fig. 31 illustrates another type of variation from figs. 27, 28. It represents the unusual carpel of *Aquilegia*. From an inspection and comparison of this figure with fig. 28, it is evident that the single strand represents the two ventral traces fused to the dorsal. Such a lateral fusion of traces cannot be considered extraordinary for two reasons. In the discussion of *Caltha*, *Hepatica*, and *Ranunculus* mention has been made of the lateral fusion of the three sepal traces to form a single strand.

Again students (15) of nodal anatomy of vegetative axes have pointed out that the three traces to a leaf may adhere from the point

of origin into the base of the leaf, thereby forming a single strand. Fig. 32 represents a carpel of *Ranunculus hispidus*. In this carpel the three traces are united from their point of origin into the base of



FIGS. 27–34.—Series of diagrams illustrating derivation of uniovulate single trace carpel from multiovulate three trace carpel: fig. 27, *Trollius;* fig. 28, *Caltha-Aquilegia;* figs. 29, 30, *Calycanthus;* fig. 31, *Aquilegia* (unusual); fig. 32, *Ranunculus;* fig. 33, *Hepatica;* fig. 34, *Thalictrum.*

the carpel, and the number of ovules has been reduced to one. Thus in this carpel the two conditions expressed separately in figs. 30 and 31 are found; namely, reduction of ovules from many to few to one,

and union of three traces to form a single strand. Fig. 33 (see also fig. 20) represents a condition in which the two ventral traces never become separated from the dorsal trace. Such a diagram depicts the conditions in *Hepatica*, *Anemone*, and *Clematis*. Two other genera, *Thalictrum* and *Anemonella*, show a slightly different type of variation from the *Caltha-Trollius-Aquilegia* type. The three traces are united into the basal portion of the carpel (fig. 34). The dorsal strand becomes a distinct strand and passes up the dorsal margin of the carpel. The two ventral strands remain as a single unit and pass up the ventral margin. Both dorsal and fused ventral strands give off lateral branches in greater numbers than any of the other Ranunculaceae. The strand passing up the ventral margin of the carpel represents the fusion of two ventral strands, because in no other form studied does a ventral trace give off branches laterally both to the right and left. Fig. 34 shows this strand as resolved into its two components. It is also to be noted that the trace to the ovule arises at a point some distance above the point of separation of the dorsal and ventral strands. This is indicative of the fact that the surviving ovule is not a basal one.

Thus anatomical studies of the carpels of the Ranunculaceae (figs. 27–34) reveal two important conclusions. (1) The two ventral traces to a carpel may become fused to the dorsal trace, thereby forming a single entering strand. (2) The uniovulate carpel can be derived from the multiovulate carpel through a gradual suppression of ovules. This conclusion is especially interesting because it is derived independently of the morphological and taxonomic evidence presented in the discussion of *Trollius* to point to a similar conclusion.

STAMEN.—The stamens, not only of the Ranunculaceae but also of angiosperms in general, so far as recorded in literature, are distinctly single trace organs. In the Ranunculaceae absolutely no branching of this trace occurs; therefore neither a pinnate nor a palmately veined ancestor can be assumed. Furthermore, this single trace gives no evidence as to whether it is a morphological unit, the remnant of a more extensive supply, or a fusion of several traces. An interpretation of the vascular condition of the stamen, therefore, is not possible on the evidence available. Thus the vascular anatomy of the staminate structures of some of the other groups of the

"primitive" dicotyledons and monocotyledons offers a field for interesting investigations in the hope of solving the problem.

PETAL.—When the anatomical data concerning the petals of the Ranunculaceae are considered, the corolla disappears as a morphological entity. The petals are sterile stamens. The evidence does not reveal the stages of this change. The suggestion is made that the petal could be derived from an expanded leaflike microsporophyll which has retained the leaflike form but lost the sporophyllaceous character; and the stamen as retaining the sporophyllaceous character but losing the leaflike form. Another possible derivation of the petal is through a loss of the anther of the typical stamen and a subsequent dilatation of the filament. More data concerning the exact nature of the stamen itself, however, must be gathered before the mode of origin of the petal of the Ranunculaceae from its microphyllous ancester can be determined. It is also to be emphasized that, whereas the petals of the Ranunculaceae are of stamen affinity, no indication exists but that the petals of some other plant groups may be sepaloid in nature rather than petaloid.

SEPAL.—In the discussion of *Caltha palustris* it was pointed out that a series could be constructed from sepals receiving three traces arising from three distinct gaps to sepals receiving three traces from a single gap (figs. 8*a*, 9, 10, 11, 8*c*, in the order named). The justification of reading the series as culminating in a three trace, single gap condition was based upon the well defined tendency among the angiosperms toward a reduction in the amount of axial woody tissue. In all of the other genera except *Trollius*, a more or less complete similar series can be constructed; but in *Hepatica* (figs. 18, 17, 16), *Ranunculus*, *Anemonella*, and *Thalictrum* the series is especially complete. In *Hepatica*, at least, evidence exists of a further modification of the primitive condition. In this genus certain sepals show evidence that the three traces arising from a common gap have fused laterally to form a single strand (fig. 19). On the other hand, the single trace sepals of *Anemonella* and *Thalictrum* are probably due to a disappearance of the lateral traces; therefore the sepals of the Ranunculaceae are fundamentally three trace organs.

It is an interesting fact that among leaves, carpels, and sepals the tendency exists toward a reduction in the number of gaps formed

by the departing traces, and a fusion or a suppression of the lateral traces. This fundamental similarity of development illustrates another phase of plant evolution, namely, that all organs of one plant are not developing in the same direction at the same time. *Hepatica*, for instance, has the most highly evolved vascular supply to the carpel of the group, a more primitive sepal condition, and a foliar condition of another degree of specialization.

SUPPRESSED ORGANS.—The presence of vascular strands to suppressed organs, such as to suppressed ovules of *Trollius* and suppressed carpels of *Caltha*, demonstrates that an organ may disappear before the vascular supply to that organ disappears. On the other hand, the vascular supply does not always lag behind; its disappearance may precede that of the organ. Unpublished observations of the writer support this latter contention. In the sterile flower of *Sassafras variifolium* (Salisb.) Ktze., a small globose pistil is present, but no vascular supply leads to it. Thus these observations upon the Ranales substantiate the statements that the vascular supply to an organ may disappear either before the organ, or after it. The third possibility (both disappearing at the same time) also occurs.

INTERRELATIONSHIPS.—Within the Ranunculaceae three or four major lines of divergence from the prototype have occurred. (1) *Caltha*, *Coptis*, *Trollius*, and *Actaea* have retained the multiovulate, three trace carpel, the spiral insertion of all parts, and the three trace sepal; they are therefore the least specialized group. (2) *Hepatica*, *Clematis*, *Anemone*, *Anemonella*, and *Ranunculus* have become specialized in that the three traces to each carpel have become fused to form a single strand, and in that the carpels are uniovulate. Within this group *Ranunculus* is the most specialized. The sepals are both whorled and five. Petals also have appeared, and are usually whorled and five in number. (3) *Thalictrum* possibly ought to be considered as a separate line of development because of its dioecious character; however it agrees with *Anemonella* in every other respect. (4) *Aquilegia* typifies the other distinct line of divergence. It has retained the multiovulate carpel receiving three distinct traces, but has become whorled as to the insertion of parts and has become arranged entirely upon the numerical plan of five. The presence of petals is also a specialized and advanced character.

Summary

As the descriptions, discussions, and general conclusions have shown, all of the 17 representative species of the Ranunculaceae studied agree as to fundamental floral vascular structure. The axis is a simple one. All floral organs are usually inserted spirally (modifications occur in *Aquilegia* and *Ranunculus*). Three types of floral organs are present: carpels, stamens, sepals. The sepals are fundamentally three trace trilacunar organs. The carpels also are fundamentally three trace trilacunar organs, and in addition are multiovulate. The uniovulate single trace carpel is derived from the former. This change has been accomplished by a gradual reduction in the number of ovules from many to few to one, and a lateral fusion of the three traces to form a single strand. Stamens are unique organs in that they always receive but a single trace. Petals are evidently modifications of stamens; hence they always differ from the sepals in being definitely single trace organs. Within this unified natural primitive family, three or four distinct lines of divergence occur: (1) *Caltha*, *Trollius*, *Coptis*, *Actaea;* (2) *Hepatica*, *Anemone*, *Clematis*, *Anemonella*, *Ranunculus;* (3) *Thalictrum;* (4) *Aquilegia*. Evidence exists also of the suppression of organs (carpels, *Caltha;* ovules, *Trollius*). Thus the aggregate of facts makes the low phylogenetic position of the Ranunculaceae more certain. This investigation also is forming the basis for another study. This is a comparative study of the vascular anatomy of the flowers of the Ranunculaceae with that of the remaining families of the Ranales and other groups considered to radiate from the "Ranalian plexus."

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MORPHOLOGY OF PREISSIA QUADRATA

ARTHUR W. HAUPT

(WITH PLATES I, II AND SIXTEEN FIGURES)

Although the structural and developmental features of many of the Marchantiales have become familiar through a number of very thorough investigations, and as a result our knowledge of the group as a whole has been greatly enhanced, some of the commonest genera have received relatively little attention. One of these is *Preissia*, a form also known as *Chomiocarpon*.

There is no doubt as to the systematic position of this genus. The gross morphological characters, which are well known, render obvious its affinities to the other Marchantiales. SCHIFFNER (45) divides the Marchantiales into the Ricciaceae and Marchantiaceae, and the latter into the three subfamilies Corsinioideae, Targionioideae, and Marchantioideae. Following LEITGEB (38), he further splits up the Marchantioideae into the Astroporae, Operculatae, and Compositae. Later workers, such as CAVERS (10) and EVANS (31), consider these groups coordinate, raising them all to the rank of families. Thus EVANS separates the Marchantiales directly into the Ricciaceae, Corsiniaceae, Targioniaceae, Sauteriaceae (Astroporae), Rebouliaceae (Operculatae), and Marchantiaceae (Compositae). There seem to be valid reasons for this grouping; certainly it is more convenient than the older system. In the present paper the term Marchantiaceae is used in this restricted sense. CAVERS includes in the family the following eight genera: *Exormotheca*, *Conocephalum*, (*Fegatella*), *Lunularia*, *Wiesnerella*, *Dumortiera*, *Bucegia*, *Preissia*, and *Marchantia*. Thus *Preissia* constitutes one of the most highly specialized members of the order. It is generally recognized that its affinity to *Marchantia* is especially close.

It appears that *Preissia* is represented by but one species, widely distributed over the Northern Hemisphere. *P. quadrata* (Scop.) Nees is the name adopted for it by EVANS (31), *P. commutata* Nees, a name used by various other writers for the same species, being relegated

by him to synonomy. EVANS considers *P. quatrata* to be the sole representative of the genus in North America. He gives its distribution as Arctic America, Canada, and the northern United States as far south as Virginia and Colorado. The species also occurs in Europe and northern Asia. SCHIFFNER (45) claims that a second species occurs in Mexico, but does not give its name. It is almost certain that he refers to *P. mexicana* Stephani, a species which EVANS regards as identical with *Marchantia chenopoda* L.

Most of the material for the present study was collected in St. Lawrence County, New York, near the village of Canton. Collections were made during September and October of 1921 and 1922, and during April, May, and June of 1922 and 1923. Excellent material was also obtained near Fort Plain in Montgomery County on July 11, 1923. In both localities the plants were growing on thin soil covering granitic rocks, usually along stream banks. *Preissia* was found in relatively drier situations than *Marchantia* and *Conocephalum*, forms which occur in the same region.

Thallus

The gametophyte of *Preissia* consists of a dorsiventral, pale green thallus with somewhat wavy margins. It is thickened along the median line, on either side forming a thin lamella. Unlike *Marchantia*, it lacks a distinct midrib. The thallus branches dichotomously when young, but later forms apical innovations, in this respect also differing from *Marchantia*. The ventral surface bears two longitudinal rows of purple scales along the median line, and both smooth and pegged rhizoids. The scales are appendaged as in the other Marchantiaceae.

The main body of the thallus consists of uniformly compact parenchyma with a single layer of air chambers beneath the epidermis (fig. 1). These arise by intercellular cleavage, the split starting below the epidermis and becoming extended to the surface. The method of air chamber formation closely resembles that described by BARNES and LAND (2) for *Marchantia*. Chlorophyllose filaments arise from the floor and sides of the air chambers; they may be either simple or branched. The epidermis consists of a single layer of thin walled cells containing relatively few chloroplasts. The thallus air

pores are of the compound or barrel-shaped type found only in *Bucegia*, *Preissia*, and *Marchantia*. In the other genera of the Marchantiaceae and in the Rebouliaceae compound air pores are limited to the receptacles. The pore opening is surrounded by 4–6 superimposed rings of cells, the lowest ring consisting of four large cells which project inward. GOEBEL (23) was the first to show that in *Preissia* these large cells are capable of causing a partial closure of the air pore when an excessive amount of water is lost from the cells of the thallus. When the latter are fully turgid the air pores are wide open. The same behavior has been described by CAVERS (9). GOEBEL also found that the air pores of *Marchantia* do not close.

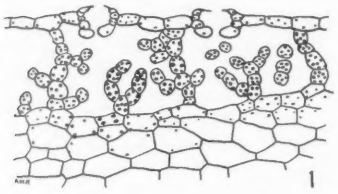


FIG. 1.—Upper region of thallus showing air chambers and pores; ×112.

Chloroplasts are found in the cells just below the air chambers, but are absent from the cells farther down. Along the median line of the thallus the colorless region comprises more than half its thickness. Here the cells become more and more elongated toward the ventral side, the lower cells being 5–10 times as long as wide. The walls of these elongated cells are slightly thickened and bear pits. The occurrence of cells similarly pitted has been reported by Miss STARR (47) in *Plagiochasma*, and by BOLLETER (4) and CAVERS (8) in *Conocephalum*. In *Preissia*, however, the cells in the ventral region are more elongated than in the other forms.

As in many other liverworts, intracellular fungi live in the lower part of the thallus. They are present chiefly along the median line and are more abundant in the older parts of the thallus. The fungal zone often constitutes one-half to two-thirds of the thickness of the thallus, thus occasionally extending as far as the air chambers, but in most cases it is more limited. In the ventral region the hyphae are arranged in parallel strands extending longitudinally; above they form compact tangled masses inside the shorter cells of the thallus. The intracellular fungi of *Preissia* have been studied by GOLENKIN (26), CAVERS (7), and others.

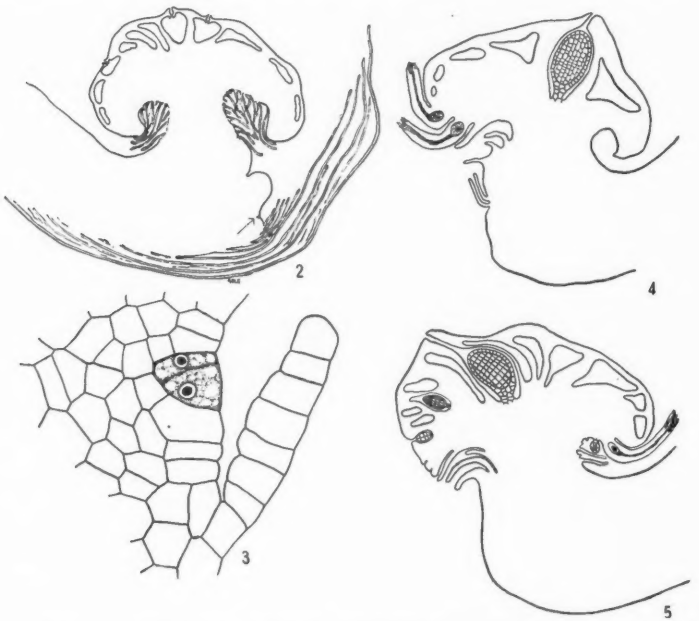
A notable feature of *Preissia* is the occurrence of scattered sclerotic cells in the ventral portion of the thallus. These were first described by GOEBEL (**22**). They are elongated, thick walled, dark brown, fiber-like cells with pointed ends. As GOEBEL reports, they ordinarily occur singly, but occasionally in cross-section two or three may be seen together. Their significance is uncertain. CAVERS (**9**) thinks that their chief function is the conduction and storage of water, pointing out that no fibers occur in plants grown in a moist atmosphere. Isolated mucilage cells are present in all parts of the thallus, but mucilage canals are absent. Starch grains do not accumulate conspicuously except in the older female receptacles, where the presence of reserve food is obviously related to the growth of the sporophytes. Oil globules are present in the apical region, especially in the epidermal cells, and in the epidermis of the receptacles.

Growth of the thallus is by means of a single cuneate apical cell which cuts off segments from its four sides (fig. 3). This is the prevailing type among the Marchantiales. The apical cell is small and not easily seen in sections through the growing notch. In most of the higher Marchantiales the formation of a receptacle terminates continued dichotomy of the growing apex. This condition prevails in *Preissia*, but here further growth of the thallus occurs through the formation of apical innovations ("ventral adventitious shoots"). Soon after a receptacle begins to form, the new shoot arises beneath it as a small rounded elevation. Below is situated the apical cell which has produced this primordium, and which continues its growth (figs. 2, 3). Apical innovations may arise beneath both male and female receptacles. The growing apex gives rise to a dorsal branch, which by further forking forms the receptacle, and a ventral branch which forms the apical innovation. The latter grows as the receptacle is developing, and later produces a new receptacle in its apical notch. In regard to the origin of the adventitious branches in *Targionia*, DEUTSCH (**13**) says that they "have absolutely nothing to do with the apical cell."

Receptacles

For the most part, the receptacles of *Preissia* are unisexual and dioecious. Only a few monoecious plants were seen, about 1 per cent in the material studied. A great many bisexual receptacles were

found, however, as will appear later. In *Preissia* both male and female receptacles are stalked. The occurrence of stalked male receptacles is an advanced feature, characteristic only of *Dumortiera*, *Bucegia*, *Preissia*, and *Marchantia*. Both kinds of receptacles repre-



FIGS. 2–5.—Fig. 2, median longitudinal section of thallus with female receptacle showing position of apical cell and origin of apical innovation, ×60; fig. 3, enlargement of fig. 2 showing apical cell cutting off dorsal segment, ×665; figs. 4, 5, young bisexual receptacles; ×75.

sent a definite branch system, terminating dichotomous apical growth of the thallus by the original apical cell, as previously explained. The stalk of the female receptacle does not begin to elongate until the sporophytes are nearly mature. In this respect *Preissia* shows a marked contrast to *Marchantia*, resembling *Asterella*, *Reboulia*, *Conocephalum*, etc.

The antheridia first appear in the late spring, the archegonia in the early summer. Sex organs continue to be formed during the

whole growing season, young archegonial receptacles appearing as late as the last of September in northern New York. The archegonial receptacles live over the winter with the sporophytes in the stage in which the sporogenous tissue has just been differentiated, as also noted by Miss GRAHAM (27). Sometimes, however, the development goes farther before winter. Growth of the sporophytes and of the receptacle stalk continues in the spring, the spores maturing in June.

Both kinds of receptacles have compound air pores like those found on the thallus, and air chambers with green filaments. In both cases the receptacle stalk has two rhizoid furrows and is without green tissue. The air chambers of the male receptacle are deep and narrow, while those of the female receptacle and thallus are alike. There are few or no chlorophyllose filaments in the deeper air chambers in the center of the antheridial disk between the pits containing mature antheridia, but only in the superficial portion of the disk. CAVERS (9) says that green filaments are absent from the margin of the receptacle, but this was not found to be the case. The male receptacles are disklike and slightly convex above with a thin margin. They are but slightly or not at all lobed. EVANS (31) notes that the antheridia occur mostly in four, sometimes 3–6 radiating rows formed in acropetal succession. The antheridial chamber opens to the top of the disk by a simple type of pore, the pore margin consisting of unthickened cells but slightly raised above the surface. In no way is the pore modified.

The female receptacles are hemispheric, with mostly four inconspicuous lobes and four prominent ridges alternating with them. These ridges are to be regarded as homologous with the conspicuously developed rays of the female receptacle of *Marchantia*. The cavity on the under side of each ridge contains a group of hairlike paraphyses (fig. 2). The archegonia arise beneath the lobes, each group being inclosed by a single membranaceous involucre having an entire margin. LEITGEB (38) has pointed out that the archegonia show a tendency toward a tangential arrangement, instead of being arranged radially as in *Marchantia*. Ordinarily about four or five archegonia are formed in each group. In this respect *Preissia* stands midway between such forms as *Reboulia* and *Conocephalum*, where normally only one archegonium occurs in each notch, and *Mar-*

chantia, where many are formed. In the material studied only one sporophyte develops under each lobe as a rule, although in rare cases two were seen under the same lobe. CAVERS (**9**) states that in most cases two sporophytes mature in each archegonial group.

Bisexual receptacles

The material collected at Fort Plain, as it occurred in the field, consisted mostly of plants bearing young receptacles having the general male form, a few plants (about 5 per cent of the total) with nearly mature male receptacles, and a very few (less than 5 per cent) with very young female receptacles. Upon sectioning the youngest male receptacles, it was found that about half of them bore both antheridia and archegonia. It was estimated that these bisexual receptacles comprised approximately 30 per cent of the total collection. It is noteworthy that none except the very youngest receptacles were bisexual.

The Canton material, collected at intervals from the middle of September to the middle of October, consisted mostly of plants bearing receptacles having the general female form. About 20 per cent of these were bisexual. There were a few old strictly antheridial receptacles, but no young ones. Still fewer old receptacles were found having elongated stalks and the typical male form, but bearing one or two (rarely three) nearly mature sporophytes. These facts indicate that the greatest proportion of strictly antheridial receptacles appears at the beginning of the season, and the greatest proportion of strictly archegonial ones at the end. It is also apparent that the greatest proportion of bisexual receptacles is found at the middle of the growing season, their number increasing to a maximum and then decreasing.

Bisexual receptacles in the Marchantiales were first reported by TAYLOR (**49**), who found them in *Dumortiera irrigua*. In a later paper (**50**) the following statement is made with reference to this species: "The fructification is commonly dioecious, sometimes monoecious, and not rarely androgynous as observed in *Marchantia androgyna*." The latter is an old name for *Preissia quadrata*. In TAYLOR'S earlier paper *Preissia* is mentioned, but nothing is said of its being androgynous.

GOEBEL (21) later studied bisexual receptacles in *Preissia*, noting that the antheridia are borne on the upper side of the anterior portion of the receptacle, and the archegonia on the under side of the posterior portion. Because the receptacles are typically unisexual, he considers that either part of a male receptacle has produced archegonial primordia which have then undergone a displacement to the lower side, or vice versa. He regards this as a mere matter of displacement which does not represent a reversion to a more primitive distribution of sex organs.

LEITGEB'S study (38) of this situation in *Preissia* differs in several important respects from that of GOEBEL. He found a large clump of plants which bore bisexual receptacles exclusively, and when grown in culture did the same thing the next year. Without exception the anterior half of each receptacle was female and the posterior half male, whereas GOEBEL had found just the opposite relation to exist. The forward portion bore two archegonial groups which corresponded in every way to the two anterior groups of a normal female receptacle, while the posterior half bore on its dorsal surface the sunken antheridia. As on a normal male receptacle, the male part of the disk had a thin margin, but this turned down on either side as it went forward to the archegonial groups. LEITGEB considers that, in the case of the bisexual receptacles, the differentiation of sex is delayed until the branches of the receptacle are formed.

ERNST (17, 18) finds that bisexual receptacles occur abundantly in *Dumortiera trichocephala* and exceptionally in *D. velutina*. The arrangement of the sex organs does not coincide with that found in *Preissia* by either GOEBEL or LEITGEB, as here on one side is seen the typical configuration of the female receptacle with archegonia, and on the other side the regular form of the male receptacle with antheridia in pits. CAMPBELL (6) confirms the occurrence of bisexual receptacles in *D. trichocephala*. CUTTING (11) observed a few cases in *Marchantia* where a female receptacle with functional archegonia produced an antheridium-bearing lobe as a proliferation from its under side. He correctly regards such cases as abnormalities and not comparable with the bisexual receptacles of *Preissia*. In GOEBEL'S study of *Monoselenium* (25) some bisexual receptacles were found with archegonia in front and antheridia behind. In his study of *Re-*

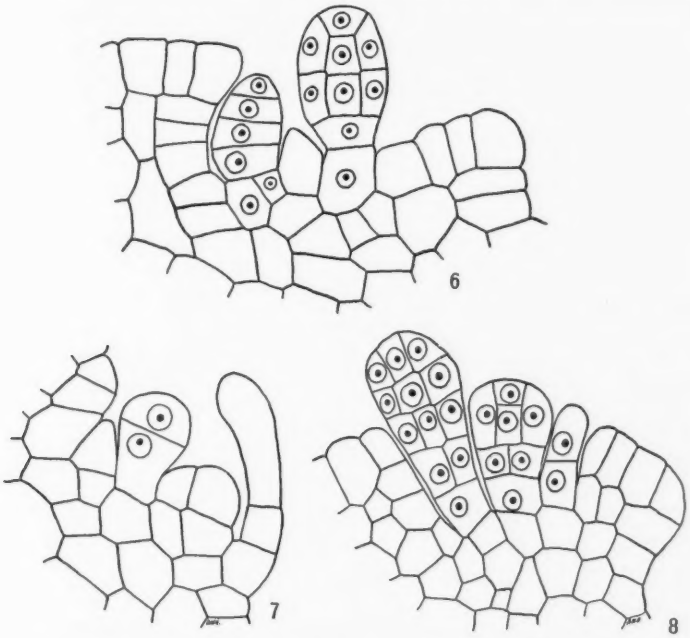
boulia, DUPLER (14) found a few female receptacles bearing male sex organs, and vice versa.

When first formed, the receptacles of *Preissia* are small rounded elevations indistinguishable from one another until the first sex organs are formed. If antheridia are first produced on a receptacle, as ordinarily happens during the early and middle part of the summer, the general form of the receptacle comes to be male, that is, the top becomes flat, the margin thin, and the air chambers deep and narrow. If sooner or later, while the receptacle is growing, archegonia arise at one or more of the growing points, a lobe forms above them, a lobe such as characterizes a typical female receptacle. This portion of the receptacle then forms shallow air chambers and becomes otherwise distinctively female. If archegonia arise on an antheridial receptacle at all, they do so while it is still relatively young. It should be understood that after a growing point has once produced archegonia, it never gives rise to antheridia again. Thus if archegonia first arise on a young receptacle at all four growing points, the receptacle assumes the typical female form. Several cases were observed in which young archegonia were arising immediately in front of young antheridia. One of the most interesting is shown by figs. 6, 7. This demonstrates conclusively that both kinds of sex organs may arise as segments of the same apical cell, and that the formation of archegonia immediately follows the production of antheridia.

In most of the bisexual receptacles examined, either both anterior groups of sex organs were of one sex and both posterior groups of the other sex, or less frequently three were of one sex and one of the other. In a few cases both of the groups on one side of the receptacle were of the same sex, and both groups on the opposite side of the other sex. The latter is similar to the arrangement ERNST found in *Dumortiera*. In no case, however, were groups diagonally opposite each other on the receptacle found to be of the same sex. In most of the preparations of young bisexual receptacles studied, and in many of the older ones, one or both of the anterior lobes were producing archegonia while antheridia were confined to the central and posterior portions of the receptacle (fig. 4). This is similar to the condition seen by LEITGEB. A few young bisexual receptacles were examined,

and some older ones, in which archegonia were being produced only under one or both of the posterior lobes (fig. 5). This coincides with the situation described by GOEBEL.

The present study of bisexual receptacles in *Preissia* justifies the



FIGS. 6–8.—Young archegonia arising on bisexual receptacle immediately in front of young antheridium; ×665; fig. 7 drawn from next section; fig. 8, young sex organs arising on bisexual receptacle: to left a transitional type, in center a young archegonium, to right an archegonium initial; ×665.

following general conclusions. (1) It seems well established that there is a definite time relation involved in the appearance of sex organs. (2) It appears certain that all of the plants contain the possibilities of producing either kind of sex organs. Although the term "dioecious" is used to describe the usual condition of sexuality in *Preissia*, sexual differentiation of thalli does not exist. (3) The general form of the receptacle is determined by the kind and number of

sex organs it produces. The receptacle of *Preissia* is a plastic structure, undifferentiated at first, and capable of assuming either male or female characters. (4) This is strongly suggestive of a common origin, phylogenetically, for the highly differentiated male and female receptacles of the higher Marchantiales. (5) As to what determines whether antheridia or archegonia shall be produced on a given receptacle, this investigation throws no light. (6) The significance of the occurrence of bisexual receptacles in *Preissia* is uncertain.

Antheridium

The antheridia arise in acropetal succession from segments of the apical cell. Their development corresponds to the regular Marchantiales type. The superficial papillate initial (fig. 17) divides transversely (fig. 18), the basal cell forming the imbedded portion of the stalk and the outer cell the rest of the antheridium. A filament of four cells is then formed from the latter by the appearance of three additional transverse walls (figs. 19–21), thus agreeing with STRASBURGER'S account (**48**) of *Marchantia*. The sequence of these walls was not apparent. The writer (**29**) has shown that in *Reboulia* there seems to be no definite sequence; at least there is not the centrifugal succession of cell walls which STRASBURGER claims for *Marchantia*. According to DURAND (**16**), the superficial portion of the antheridium of *Marchantia* at this stage probably consists of but three cells. He observed no young antheridium with more than two transverse walls in its superficial portion. ABRAMS (**1**) found the same situation in *Cryptomitrium*.

Vertical walls are now formed in two planes at right angles to each other (figs. 22–24). These commonly appear first in the basal tiers, but often elsewhere, as reported by DURAND (**16**) for *Marchantia* and by the writer (**29**) for *Reboulia*. In the latter the appearance of the first vertical walls immediately following the formation of four tiers of cells in the superficial portion of the antheridium has been shown to be a constant feature. Furthermore, both DURAND and the writer find that following the appearance of the first vertical walls, additional transverse walls may come in, resulting in the formation of five or six tiers of cells. This may also take place in *Preissia* (figs. 25, 26).

In a recent study of *Reboulia*, DUPLER (14) confirms the development of the antheridium described by the writer, but finds that occasionally four transverse walls may be formed in the upper cell before the vertical walls appear. CAMPBELL (5) reports a similar condition in *Asterella*. BOLLETER (4) finds that in *Conocephalum* three or four transverse walls appear as a rule, but that the young antheridium may consist of as many as eight superimposed cells before the vertical walls come in. It is likely that this may happen in other Marchantiales, but was not observed in the present study.

As in *Reboulia*, the formation of periclinal walls cutting off the sterile jacket from the inner spermatogenous cells involves only the three uppermost tiers, the lower cells contributing to the stalk (fig. 27). This is apparent even in older antheridia, because the original division walls often stain more heavily than the later ones (fig. 28). Further growth of the spermatogenous tissue is typical, and need not be described.

CAMPBELL (5) states that in *Riccia* "the lower one or two segments and the terminal ones do not take part in the formation of sperm cells, but simply form part of the wall of the antheridium." ABRAMS (1) finds the same unusual situation in *Cryptomitrium*. He states that the spermatogenous tissue is derived exclusively from the middle of the three original cells into which the superficial portion of the young antheridium is divided, the upper and lower cell taking no part but contributing to the antheridium wall. Miss MCFADDEN (41) reports a similar condition in *Targonia*. This behavior is not in agreement with any other investigation on the Marchantiales. That the upper cell of the young antheridium does contribute to the spermatogenous tissue is strongly suggested by a careful examination of consecutive stages in both *Reboulia* and *Preissia*, but the critical mitotic figure to establish the point was not found in these forms. Among the writer's preparations of *Marchantia polymorpha*, however, an antheridium was found which definitely proves the case (fig. 29).

Archegonium

The archegonial receptacle arises at the growing point of the thallus as a small rounded knob, and, as in all of the higher Marchantiales, the apical cell is involved in its formation. A new apical cell forms in each receptacle notch, of which in *Preissia* there are four.

The archegonium initials do not appear until the young receptacle is conspicuously dome-shaped. The superficial papillate initial (fig. 32) undergoes a transverse division, forming a basal and an outer cell (fig. 7). The latter gives rise to the primary axial cell and the primary wall cells, by the development of three vertical walls in the way characteristic of all Bryophytes (figs. 33–34). At the same time the basal cell commonly divides by a transverse wall.

This sequence of wall formation (except that in some cases the basal cell does not divide) has been reported by JANCZEWSKI (33) for *Riccia*, by CAMPBELL (5) for *Riccia*, *Targionia*, and *Asterella*, by GARBER (20) and LEWIS (39) for *Ricciocarpus*, by LANG (37) for *Cyathodium*, by ABRAMS (1) for *Cryptomitrium*, by Miss STARR (47) for *Plagiochasma*, by HAUPT (29) for *Reboulia*, by CAVERS (8) for *Conocephalum*, and by DURAND (16) for *Marchantia*. STRASBURGER (48) states that in *Marchantia* the outer cell undergoes a transverse division before the three vertical walls appear. The same condition has been reported by JANCZEWSKI (33) for *Preissia* and *Lunularia*, and by BOLLETER (4) for *Conocephalum*. In none of these cases, however, are mitotic figures shown as proof, and hence the orthodox interpretation is possible.

Further development of the archegonium of *Preissia* is in agreement with the usual Marchantiales situation (figs. 34–39). After the primary neck canal cell has given rise to four neck canal cells by two successive divisions (figs. 37, 38), the primary ventral cell forms the ventral canal cell and egg (fig. 39), as previously reported for *Preissia* by JANCZEWSKI (33). The first division of the primary neck canal cell is accompanied by the formation of a vertical wall in the cover cell (fig. 37). Miss STARR (47) has shown that in *Plagiochasma* eight neck canal cells are formed before the primary ventral cell divides. In *Reboulia* (29) the situation is similar to that in *Preissia*, but the number of neck canal cells is later increased to 18–20. CAVERS' (8) figures show that in *Conocephalum* the primary ventral cell divides after only two cells have been formed from the primary neck canal cell, while BOLLETER'S (4) figures show that the development is normal. Both JANCZEWSKI (33) and DURAND (16) state that in *Marchantia* the primary ventral cell may occasionally divide prematurely.

The stalk of the mature archegonium is short. The neck curves

outward and upward, as in other forms where the receptacle stalk does not elongate until the sporophytes are approaching maturity. The mature archegonium of *Preissia* invariably contains four neck canal cells (fig. 39). It may also be stated with certainty that this number is not increased by later divisions, as in *Reboulia*. As in the other Marchantiales, the neck shows six cells in cross-section.

The range in variation among the Marchantiales in regard to the number of neck canal cells is shown in table I. It will be noted that the prevailing number is four, although some forms show the more primitive number eight. *Reboulia* is the only form credited with a larger number.

TABLE I

NUMBER OF NECK CANAL CELLS IN MARCHANTIALES

GENUS	WRITER	NUMBER REPORTED
Riccia	Janczewski, Campbell	4
Ricciocarpus	Garber, Lewis	4
Cyathodium	Lang	8–9
Plagiochasma	Janczewski	4
Plagiochasma	Starr	8
Cryptomitrium	Abrams	8
Reboulia	Janczewski	4
Reboulia	Haupt	18–20
Conocephalum	Cavers, Bolleter	8
Lunularia	Janczewski	4
Preissia	Janczewski, Haupt	4
Marchantia	Janczewski, Durand*	4

* Sometimes six or seven nuclei.

Anomalous sex organs

In a form having bisexual receptacles, like *Preissia*, the finding of occasional aberrant sex organs might be expected. That they have been reported in other Bryophytes is a matter of common knowledge. A few interesting cases were seen during the course of the present investigation which will be described briefly. As already pointed out, there is a definite time relation in the appearance of sex organs on the bisexual receptacles, the antheridia always developing first. It has been seen that in some cases the young archegonia and antheridia arise side by side (fig. 6). Ordinarily these are easily recognizable as either male or female organs, but sometimes young sex organs are seen which do not correspond to either type. It is impossible to say

into what kind of organ these aberrant forms might have developed. Presumably they would eventually have produced either sperms or eggs, but this could not be determined at their present stage of development. Thus in fig. 8 the oldest organ might be either an antheridium or an archegonium. The middle one is unquestionably an archegonium, and the youngest an archegonium initial. This particular receptacle had already borne antheridia. Thus the oldest organ represents a transitional type.

Fig. 40 represents an organ produced on a male receptacle. It shows no resemblance to an archegonium, and yet it is very unlike a typical young antheridium. It probably would have developed into an antheridium of an unusual kind. Just to one side of this organ, nearer the center of the disk, was seen a peculiar antheridium (fig. 41) with a restricted group of spermatogenous cells; its upper portion was prolonged into a neck which projected slightly out of the antheridial chamber.

Fig. 42 is a strictly median longitudinal section through an organ found on a female receptacle. It was borne in the position of an archegonium, yet had somewhat the appearance of an antheridium. If it were to be a normal antheridium, it should be sunken in its pit by this time. It would be interesting to determine, were it possible to do so, whether this organ would produce sperms or an egg.

The most interesting anomaly is shown by fig. 31. Here is an organ developed in a typical antheridial chamber, with a stalk half its length, and with an axial row of three cells surrounded by a sterile jacket. From a careful examination of the preceding and following section, it may be said that the sterile jacket consists of either five or six rows of cells. This organ seems to be an antheridium developing as an archegonium, a truly transitional form. The axial row consists of protoplasm which stains more densely than the other cells; in fact, it has every appearance of a young archegonium as represented by fig. 37, with the exception of its very long stalk and position in an antheridial pit. Just what was the appearance of this organ at an earlier stage of development can only be conjectured. Had development proceeded, it seems very likely that it would have become an egg producing organ.

Based on studies both in the Bryophyta and Pteridophyta, a

great deal of evidence has accumulated in support of the view that phylogenetically the canal cells are eggs which have ceased to function, and that the antheridium and archegonium are homologous organs, the spermatogenous tissue of the former corresponding to the entire axial row of the latter. This evidence has been derived chiefly from a study of abnormalities in development. The subject is well discussed in papers by GOEBEL (**24**), DAVIS (**12**), HOLFERTY (**32**), Miss LYON (**40**), MEYER (**43**), KURSSANOW (**36**), FLORIN (**19**), and others. Striking evidence that the antheridium and archegonium have had a common origin is seen in the occurrence of bisexual organs described by HOLFERTY, MEYER, and others, where the same gametangium may produce both eggs and sperms. The present study of *Preissia* adds evidence of a new sort to the view that the two kinds of sex organs of Bryophytes are homologous.

Fertilization

A great many cases of fertilization were observed in material collected September 24, 1921, at Canton, New York. Practically all of these were in the same condition, the male nucleus within the egg and in contact with the female nucleus, but not yet fused with it. This stage has been observed by Miss BLACK (**3**) in *Riccia*, by GARBER (**20**) in *Ricciocarpus*, by MEYER (**42**) in *Corsinia*, and by WOODBURN (**51**) and DUPLER (**15**) in *Reboulia*. Judging from the frequency of this stage in my preparations, it seems very likely that the sperm and egg nuclei do not fuse immediately upon coming together, but remain in contact for a while.

Before the entrance of the sperm, the chromatin of the egg nucleus surrounds the nucleolus as a dense mass (fig. 39). Only two cases were observed in which the male and female nuclei had not yet come into contact. In both instances the chromatin of the egg nucleus was in the form of a reticulum (fig. 43). Of the many cases seen in which the sexual nuclei were in actual contact, the chromatin of both nuclei was reticulate in only four cases (fig. 44), while in twenty-one cases in both egg and sperm it was contracted into a dense mass around the nucleolus (fig. 45). It seems likely that the latter represents the more advanced condition of development.

Miss GRAHAM (**28**) has described and figured centrosomes in

Preissia at the time when the male and female nuclei come together. She saw centrosomes with astral rays at either pole of the egg nucleus. After a critical examination of all available fertilization stages, the writer demonstrated to his own satisfaction the presence of centrosomes such as Miss GRAHAM describes in about ten cases out of forty (fig. 45). In some instances, as in fig. 43, the centrosomes were above and below the egg nucleus, thus appearing in the preceding and following section. Miss GRAHAM speaks of the egg cytoplasm as consisting of an inner granular zone and an outer coarsely vacuolar zone. It seems to the writer that her use of the term "zones" is forced. A greater concentration of cytoplasm around the nucleus is perfectly apparent, but it does not constitute a definitely delimited portion of the cell such as the term "zone" implies.

In many cases the cytoplasm is particularly dense between the fusing nuclei (figs. 43–44). In regard to this matter Miss GRAHAM states:

> Between the antherozoid and the egg nucleus lies a small mass or body unlike the cytoplasm just described. From its position in close proximity to the nucleus of the antherozoid, the small quantity visible, and the absence of similar cytoplasm anywhere else in the cell, it might be thought to be cytoplasm brought in by the antherozoid, but I have no proof that this is the case.

Miss GRAHAM does not explain why there should be so much of this male cytoplasm and why it should be pushed ahead of the sperm nucleus. Her interpretation on this basis of the presence of dense cytoplasm at a place of high metabolic activity seems to be entirely without evidence.

Chromosome number

Although a great many mitotic figures were observed in the preparations, in only a very few cases could the chromosomes be counted. Miss GRAHAM (**27**) made a very thorough study of mitosis in *Preissia* without discovering the chromosome number. She states that it is probably eight, but does not give convincing evidence. The chromosomes in the vegetative cells are described and figured as small oval bodies, as seen in both side and polar view. In her study no centrosomes were seen.

A number of particularly clear polar views of mitotic figures were seen in a half-grown antheridium occurring with others on a

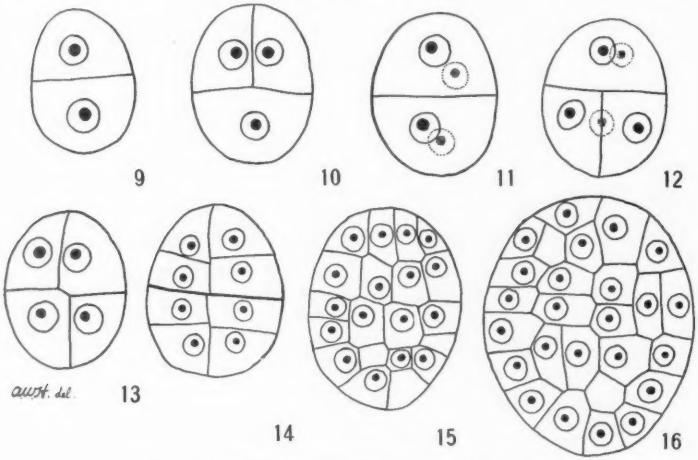
bisexual receptacle. The chromosomes were entirely separate from one another and sharply stained. The haploid number is unquestionably nine (fig. 30). One chromosome is much smaller than the others, being nearly spherical. The others are five to ten times as long as wide. Unfortunately, cases favorable for counting were not found on other preparations; hence it cannot be stated whether or not there is any relation between the sexual condition of a given plant and its chromosome equipment.

SHOWALTER (46), studying *Conocephalum conicum*, a dioecious species, found no visible differences between the sexes. He demonstrated that the chromosome number is nine instead of eight, as reported by earlier workers, and that one of the chromosomes is much smaller than the others. *Conocephalum* and *Preissia* are therefore alike in this respect. Chromosome numbers have not been determined in a large number of the Marchantiales. Miss BLACK (3) reports eight for *Riccia Frostii*, LEWIS (39) and GARBER (20) four for *Ricciocarpus*, and MEYER (42) eleven for *Corsinia*. The numbers given are for the gametophyte.

Embryo

The first wall to be formed in the fertilized egg is transverse (fig. 9), or sometimes slightly oblique, and results in two approximately equal segments. Each cell then divides by a vertical wall, and later by another vertical wall at right angles to the first one, resulting in the formation of an octant (figs. 10–13). This behavior has been reported by KIENITZ-GERLOFF (34) for *Riccia*, by CAMPBELL (5) for *Riccia*, *Targionia*, and *Asterella*, by MEYER (42) for *Corsinia*, by LANG (37) for *Cyathodium foetidissimum*, by ABRAMS (1) for *Cryptomitrium*, and by KIENITZ-GERLOFF (34) and DURAND (16) for *Marchantia*. KIENITZ-GERLOFF (34, 35) states that the same type of development prevails in *Preissia* and possibly in *Grimaldia*, but his figures do not show the earliest stages. Further divisions occur in both the hypobasal and epibasal portions of the embryo, resulting in a more or less globular mass of cells (figs. 14–16). It has been shown by KIENITZ-GERLOFF (35) in *Preissia* and by DURAND (16) in *Marchantia* that the capsule is derived from the epibasal cell, and the foot and seta from the hypobasal.

As demonstrated by WOODBURN (51), HAUPT (30), and DUPLER (15), the embryo of *Reboulia* develops without the formation of an octant stage, the first three walls being transverse. BOLLETER (4) finds a similar condition in *Conocephalum*. LANG (37) finds a quadrant in *Cyathodium foetidissimum*, and a filament of four cells in *C. cavernarum*. Although CAMPBELL (5) finds an octant stage in *Targionia hypophylla*, Miss O'KEEFFE (44) states, "No such stage was observed, all the young embryos seen consisting of a single row of as many as five cells, but more often either three or four, before any longitudinal



FIGS. 9–16.—Stages in development of embryo; ×450

divisions had taken place." Miss STARR (47) figures just one embryo of *Plagiochasma*, which indicates that its development resembles that of *Reboulia*. In *Dumortiera*, CAMPBELL (6) finds that the first two walls are transverse, and that "it is not unlikely" that another transverse wall may appear before the coming in of the vertical walls. In *Ricciocarpus*, GARBER (20) finds that the young embryo may consist of either a quadrant or a row of four cells. In *Conocephalum*, CAVERS (8) reports that the first wall is transverse. Sometimes a second transverse wall appears in the epibasal cell, but usually the next walls are vertical, dividing the embryo into an octant.

DUPLER (15) claims that occasionally a functioning triangular apical cell may be formed in the young embryo of *Reboulia*, the em-

bryogeny thus showing "an occasional partial agreement with that characteristic of the Musci." He also finds a triangular cell at the base of the embryo in some cases. This had earlier been reported by WOODBURN (51) and disputed by HAUPT (30). Because the vertical axis of the elongated embryo of *Reboulia* is often not straight but slightly curved, and because any of the walls may be somewhat inclined (not always perpendicular to the others), sections often reveal the presence of a triangular cell at either end of the embryo. Thus it appears when an anticlinal wall intersects one of the first vertical walls if either be slightly curved.

The writer has observed the same thing in the present study. It is also shown by the figures of other investigators, such as DURAND'S (16) figs. 84 and 86, KIENITZ-GERLOFF'S (35) figs. 3*A* and 6, and MEYER'S (42) figs. 6, 7, 8, etc., but none of these authors claims that a "functioning apical cell" exists. Concerning the early embryo of *Targionia*, CAMPBELL (5) writes as follows:

> In no cases seen was there any indication of a two-sided apical cell such as HOFMEISTER figures for *Targionia*, and probably his error arose from a study of forms where the quadrant walls were somewhat inclined, in which case the intersection of one of the secondary walls with it might cause the apex of the embryo to be occupied by a cell that, in section, would appear like the two-sided apical cell of the moss embryo.

KIENITZ-GERLOFF (35) finds in both *Preissia* and *Grimaldia* that the triangular cell often formed at the apex of the young embryo is not an apical cell. Regarding the embryo of *Preissia*, he writes as follows:

> Die betreffenden Querwände verlaufen indessen selten horizontal, meist schliessen auch sie mit der Verticalen einen mehr oder weniger spitzen Winkel ein und so erhält man häufig, sowohl auf Aussenansichten, wie auf Längsschnitten am Scheitel des Embryo das Bild einer durch zwei entgegengesetzt geneigte Wände eingeschlossenen Scheitelzelle, ein Bild, das noch täuschender wird, wenn sich an die letzt entstandene, oberste Querwand wiederum eine zum Scheitel verlaufende, tangentiale ansetzt. Es hat in diesem Falle ganz den Anschein, als ob der Embryo in der That mit zweischneidiger Scheitelzelle wüchse (Taf. IX. fig. 6), und Bilder dieser Art sind es offenbar gewesen, welche Hofmeister veranlassten, für den Marchantiaceen-Embryo ein derartiges Wachstum anzunehmen. Dass ein solches nicht Statt hat, das lehrt uns einerseits die meist noch an älteren Stadien durch ihre bedeutende Stärke hervortretende Quadranten- und Octantenwand, andererseits jede Drehung des Embryo um seine Längsaxe.

Older sporophyte

The later development and mature characteristics of the sporophyte of *Preissia* present no striking features. The mature capsule is spherical, the seta relatively short, and the foot bulbous. The capsule wall is composed of a single layer of cells except at the apex. There a cap is present three or four cells thick in the middle. Annular bands are present in the capsule wall. CAVERS (9) has shown that a few fixed elaters are attached to the apical cap, and that fixed elaters may also arise from the base of the capsule. As in *Marchantia*, a perianth is formed around the sporophyte.

Summary

1. *Preissia* comprises a single species, *P. quadrata*, closely related to *Marchantia*.

2. The thallus is dichotomous when young, later forming apical innovations. It lacks a distinct midrib. Both smooth and pegged rhizoids and appendaged scales are borne below.

3. There is a single layer of air chambers with green filaments; their origin is schizogenous. The epidermal cells are thin walled and contain few chloroplasts. All air pores are barrel-shaped.

4. The colorless ventral cells are elongated and have thickened pitted walls. Scattered sclerotic cells occur in the ventral region.

5. Growth is by means of a single cuneate apical cell. After a receptacle has arisen, another apical cell forms an apical innovation which continues growth of the thallus.

6. The receptacles are mostly unisexual and dioecious, rarely monoecious, but very commonly bisexual. Both male and female receptacles are stalked, and both represent a branch system. Elongation of the female receptacle stalk is delayed.

7. Both receptacles have four growing points as a rule, the male showing greater variability in this respect than the female. The female receptacle has four inconspicuous lobes and four prominent ridges, the latter being incipient rays. Ordinarily about four or five archegonia are formed in each of the four groups.

8. A greater proportion of antheridial receptacles appears during the early part of the growing season, and of archegonial ones dur-

ing the latter part. The greatest proportion of bisexual receptacles occurs during the middle of the season.

9. On bisexual receptacles the production of antheridia always precedes the formation of archegonia.

10. All of the thalli contain the potentialities of either sex.

11. The general form of a receptacle is determined by the kind and number of sex organs it produces.

12. The antheridia develop like those of the other Marchantiales. The formation of periclinal walls delimiting the spermatogenous cells involves the three uppermost tiers of cells of the young antheridium.

13. Early development of the archegonium is typical. The ventral canal cell and egg are differentiated after four neck canal cells are formed; this number is not later increased.

14. Several anomalous sex organs are described, giving evidence as to a common origin phylogentically for the antheridium and archegonium.

15. At the time of fertilization, at least in some cases, there is a centrosome with astral rays at opposite poles of the egg nucleus. The condition of the nucleus and cytoplasm at this time is described.

16. The haploid number of chromosomes is nine, one being very small.

17. The embryo develops with the octant stage characteristic of certain related genera. A functioning apical cell does not occur in the embryo of the Marchantiales.

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EXPLANATION OF PLATES I, II

All figures except fig. 29 are of *Preissia quadrata*.

FIGS. 17–28.—Stages in development of antheridium.

FIG. 17.—Antheridium initial; ×665.

FIG. 18.—First division of same into basal and outer cells; ×665.

FIGS. 19–21.—Division of outer cell to form filament of four cells; ×665.

FIGS. 22–24.—Formation of vertical walls; ×665.

FIGS. 25, 26.—Appearance of additional transverse walls; ×665.

FIG. 27.—Completion of periclinal wall formation; ×665.

FIG. 28.—Slightly older stage; ×665.

FIG. 29.—Young antheridium of *Marchantia polymorpha* showing formation of periclinal walls in upper cells; ×665.

FIG. 30.—Cells from half mature antheridium showing eight large chromosomes and one small one; ×3000.

FIG. 31.—Sex organ showing both male and female characters; ×665.

FIGS. 32–39.—Stages in development of archegonium.

FIG. 32.—Archegonium initial; ×665.

FIG. 33.—Formation of primary wall cells and division of basal cell; ×665.

FIGS. 34, 35.—Formation of cover cell and central cell from primary axial cell; ×665.

FIG. 36.—Formation of primary neck canal cell and ventral cell from central cell; ×665.

FIGS. 37, 38.—Division of primary neck canal cell to form four neck canal cells, and formation of vertical wall in cover cell; ×665.

FIG. 39.—Mature archegonium showing differentiation of ventral canal cell and egg from ventral cell; ×665.

FIG. 40.—Young sex organ developed on male receptacle; ×665.

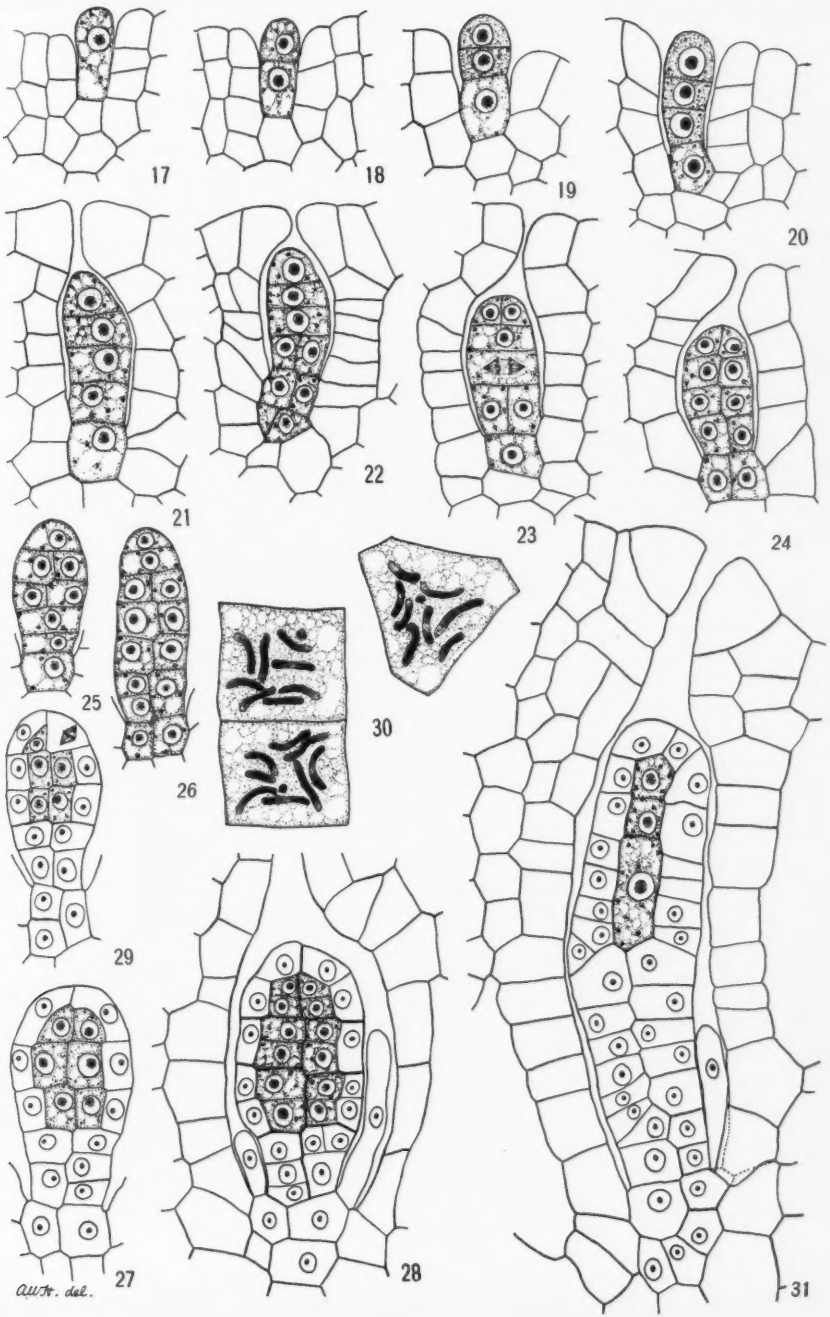
FIG. 41.—Older sex organ from same receptacle; ×665.

FIG. 42.—Median section of sex organ formed on female receptacle; ×665.

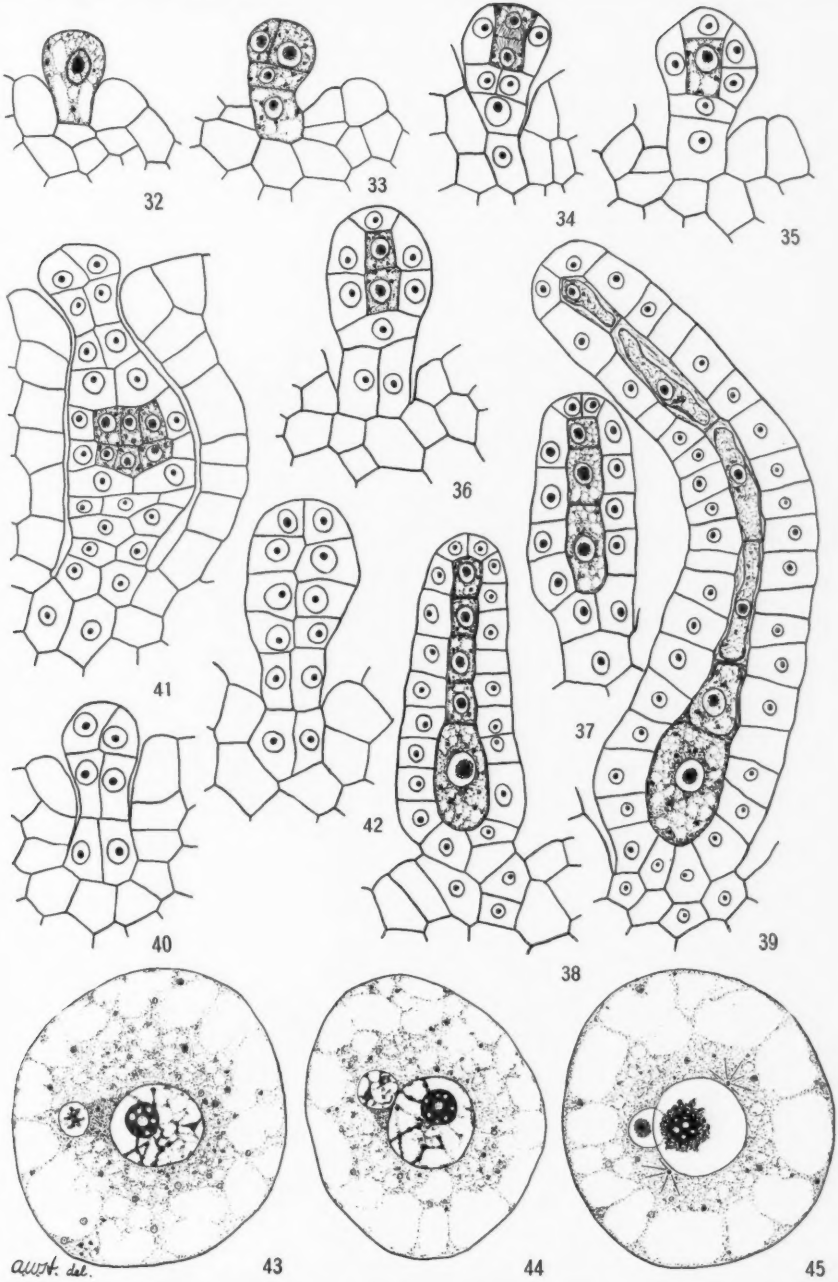
FIG. 43.—Egg with male nucleus not yet in contact with female nucleus; centrosomes in preceding and following sections above and below egg nucleus; ×1000.

FIG. 44.—Male and female nuclei in contact; no centrosomes apparent; ×1000.

FIG. 45.—Male and female nuclei in contact; centrosomes visible at opposite poles of egg nucleus; ×1000.



HAUPT on PREISSIA QUADRATA



HAUPT on PREISSIA QUADRATA

CYTOLOGICAL STUDY OF MEIOSIS IN ANTHERS OF OENOTHERA MURICATA

RALPH E. CLELAND

(WITH PLATES III, IV)

Introduction

The species to be discussed in this paper is the *O. muricata* of DE VRIES' *Mutationstheorie* and *Gruppenweise Artbildung*, a species that BARTLETT (1) considers to be different from *O. muricata* Linn., and to which he has given the name *O. syrticola*. For certain reasons I shall retain the name *muricata*, but wish to make it clear that we shall be dealing with the *O. muricata* of DE VRIES' cultures.

Material was collected during the summers of 1919 and 1920 in the experimental gardens of B. M. DAVIS. A number of collections were made from several individuals. The strain chosen was a selfed line that originated in 1912 from seed obtained from DE VRIES. The most satisfactory fixative was found to be one of ALLEN'S modifications of Bouin's solution (CLELAND 4). Unmodified Bouin gave good results also, but strong and weak Flemming both failed. The critical stages of late prophase and the heterotypic metaphase were plentifully obtained in three of the collections. Two of these were made in 1919, and include material from several individuals. The third, made in 1920, was obtained wholly from one plant.

Description

The earlier stages in meiosis have proved to be essentially identical in the various species of *Oenothera* that I have thus far described in detail. Nevertheless I have thought it advisable to examine them with care in *muricata* also. This study, however, has led to no new discoveries. So far as I can learn, there is nothing in the appearance or behavior of the pollen mother cells during the stages up to and including second contraction to distinguish *muricata* from the rest of the species investigated; consequently it will be unnecessary at this time to give a detailed account of early prophase.

Earlier papers may be referred to for figures and descriptions, which will apply to *muricata* as well. I wish merely to emphasize the fact that all of these stages give evidence that the meiotic process is telosynaptic rather than parasynaptic. In the presynizetic period, as well as in synizesis, the amount of parallelism that may be seen among the threads is not greater than would naturally be expected as a result of the contractions and condensation going on at this time. In the hollow spireme stage the threads are uniformly single (fig. 1); a case of parallelism is a rarity. The frequent appearance of splits or of approximations such as characterize the diplotene stage in many organisms is conspicuous by its absence. Furthermore, second contraction seems to witness to the presence of telosynapsis, inasmuch as splits in the threads fail to appear during this stage, and the chromosomes seem to be formed by a segmentation of the spireme as a whole, rather than from split halves of the threads. In early contraction stages, there are a number of radiating peripheral loops (fig. 2), which, as condensation proceeds, are more and more reduced, in many cases becoming at last entirely absorbed into the contracted mass at the center. In many cases the loops do not shrink to the same degree, however, so that they are visible throughout the whole of the contraction period (figs. 3–5), and it is possible to trace the direct transformation of certain of the univalent chromosomes from the exposed portions of these. The threads composing these loops, therefore, are without much doubt univalent in character.

LATE PROPHASE.—With the unfolding of the second contraction knot, there appear for the first time peculiarities in the behavior of the chromatin material which distinguish *muricata* from the other species of *Oenothera* so far studied cytologically. It soon becomes evident that the univalent chromosomes which are emerging, for the most part at least, are unpaired and attached end to end like a string of sausages. In a short time the chromosomes begin to take the form of a figure 8, four chromosomes in one circle and ten in the other, the circles being attached at one point. This attachment breaks shortly, however, and the final arrangement is found to be a single closed circle of fourteen chromosomes (figs. 6–10). In some cases the circle breaks open, and a chain of fourteen chromosomes instead of a circle is the result (figs. 11, 12). There are no paired

chromosomes at this stage. In this respect, *muricata* resembles *biennis* and *biennis sulfurea* (CLELAND **6**), the last two, however, possessing two circles instead of one. This stage corresponds to what is called diakinesis in most plants, but the entire absence of paired homologous chromosomes is in complete contrast with the close pairing and wide separation of the pairs so characteristically found in other forms. The term diakinesis can hardly be used in connection with *O. muricata*.

It is obvious that the larger the circle of chromosomes, the more difficult it will be to find cells in which the circle is both intact and wholly clear. In the first place, such an appearance may only be expected in cells whose nuclei are uncut and complete in one section. In the second place, a circle of this size is naturally much contorted as it lies within the nucleus, and, except in unusually favorable cases, certain parts of the spireme will lie above other parts, and make it difficult or impossible to trace out the whole circle chromosome by chromosome. Consequently it is not to be expected that the whole of the intact circle will be observed in a large percentage of the cells examined. There should be a considerable proportion of cells, however, in which the end to end arrangement can be observed in the case of a large majority of the chromosomes; and almost every cell should display at least some of the chromosomes thus attached. Moreover, in no case should a single instance of paired chromosomes be found. A tabulation of the best cells discovered is presented in table I. Only those concerning which there was no question of interpretation have been included in this table. The positions on the slides have been recorded in the case of most of them, so that they can be found again.

In addition to the cells included in this table, hundreds of others have been studied in which smaller parts of the circle or chain have been visible. Five or six chromosomes can often be seen in one part of a nucleus attached end to end, and in another region three or four more are found similarly joined; but a tangle in the chain at one point makes it impossible to complete the picture. Such cells have not been included in table I. On the negative side, it should be emphasized that the most careful search has failed to reveal a single instance of paired chromosomes. Furthermore, there has been no

evidence of the existence of more than one circle or chain in any of the cells studied. On the other hand, we have a certain number of cells in which all fourteen chromosomes are clearly seen, and in all of these the whole chromosome complex is arranged into a single circle or chain. In addition, most of the other cells furnish evidence, more or less complete, of the entire absence of pairing, and the constant arrangement of the chromosomes into one series. I think that it may safely be assumed, therefore, that the chromosome arrangement at

TABLE I

CHROMOSOME ARRANGEMENT IN LATE PROPHASE IN OENOTHERA MURICATA

DESCRIPTION	NUMBER OF CELLS	
Circle of 14, intact	21	
Chain of 14	11	
	Total..	32
13 chromosomes in continuous end to end series, fourteenth missing	3	
12 chromosomes in continuous end to end series, others missing	11	
11 chromosomes in continuous end to end series, others missing	7	
10 chromosomes in continuous end to end series, others missing	15	
9 chromosomes in continuous end to end series, others missing	12	
8 chromosomes in continuous end to end series, others missing	13	
7 chromosomes in continuous end to end series, others missing	10	
	Total..	71
		103

this time is constant, and typical of the species; and, in this respect, *muricata* resembles the species previously studied.

The stage under discussion lasts a relatively short time. It marks the final disappearance of the nucleolus, and in addition is characterized by a gradual reduction in size of the chromosomes. For a time they may vary slightly in size and form. These differences gradually disappear, however, as the chromosomes become reduced, until finally they are uniform and individually indistinguishable. I am strongly inclined to believe that no significance is to be attached to form and size differences observed during this period. Such slight variations as are present are bound to occur as the chromosomes become smaller, unless the rate of shrinkage is precisely the same in the various chromosomes, which is extremely unlikely.

HETEROTYPIC METAPHASE.—A multipolar spindle is formed at the end of prophase, closely investing the nucleus, of which the membrane finally disappears. The spindle fibers penetrate the substance of the erstwhile nucleus, and some become attached to the chromosomes. These are now greatly reduced in size, but are still attached end to end, and the circle is still intact. So long as the spindle is multipolar in form, the circle lies in a heap in its center, without visible orientation (fig. 13). As it becomes bipolar, however, the chromosomes comprising the circle begin to assume definite positions with reference to the poles. Spindle fibers are found to have attached themselves in such a way that adjacent chromosomes are destined to pass to opposite poles, every second chromosome, therefore, being caught by fibers leading to the same pole (figs. 14–17). The behavior is identical with that described already for *O. franciscana sulfurea* (CLELAND 2), and for *O. biennis* and *O. biennis sulfurea* (6). In metaphase the same striking regularity is found that is so characteristic of these species. The chromosomes, attached to the fibers at about the midregion, are V-shaped. The fourteen V's are attached end to end, with the apices of adjacent chromosomes pointing to opposite poles. A regular zigzag appearance is thus observed, the circle as a whole lying horizontally across the equatorial region.

Owing to the fact that all fourteen chromosomes are associated into one group, making a rather extensive circle or chain, some contortion (as seen in polar view) is usually present. The commonest appearance presented in polar view is that of a circle, one side of which has been pushed in toward the center. Such an arrangement makes it more difficult to get complete pictures in side view, inasmuch as it may result in as many as four chromosomes lying one over the other at a certain point. It is often difficult, if not impossible, to distinguish between these with certainty, and it is still harder in such cases to distinguish the attachments between adjacent chromosomes. For this reason, the percentage of cells in which it is possible to trace out the whole circle is somewhat smaller than it would be if there were no such contortion.

In *muricata*, as in other species with large circles, a certain proportion of cases is found with irregularities in this zigzag arrangement. These cases conform to the types described in former papers.

Two adjacent chromosomes at one point in the circle may pass to the same rather than to opposite poles, and at another point two other adjacent chromosomes are found to pass to the other pole (fig. 18). Or a chromosome may be suspended between the poles, without any fiber attachment, its next neighbors on either side passing to opposite poles, and an adjacent pair at some other point passing to one pole, rather than separating. Or again, two chromosomes in different parts of the circle may be suspended (fig. 19). It is perhaps not possible to state accurately the percentage of cases in which irregularity occurs, inasmuch as the circles in a large proportion of the cells are incapable of certain and complete resolution. Some idea may be obtained indirectly, however, through a study of interkinesis, and a determination of the percentage of cells showing irregular chromosome numbers. Out of 683 such cells, sixty-two were found in which the number of chromosomes in one nucleus was six, and in the other eight, or a little less than 10 per cent. Inasmuch as irregularities in the zigzag arrangement do not necessarily result in unequal numerical distribution, however, it is to be expected that the total of irregularities will be somewhat higher than 10 per cent. This is borne out by the data in table II.

In order to make the evidence upon which I have based the description of the heterotypic metaphase as quantitative as possible, a complete survey has been made of the best slides containing this stage. Every cell in metaphase has been examined, and the condition noted in all cases where the cells were complete and in side view, and sufficiently clear to afford evidence of the chromosome arrangement. The result is contained in table II, which gives some idea of the probable percentage with which irregularity occurs in the zigzag arrangement. In part A of the table, the percentage of cells containing irregularity is 24.1. In parts B and C, the percentage of cells showing eight or more visible chromosomes in one continuous series is 22.2. Cells in which the visible chromosomes were located in different parts of the circle, down to and including those showing four in one region and four in another, display irregularity in 20 per cent of the cases. As a whole, therefore, the data suggest that irregularity in the zigzag arrangement occurs in approximately one-fifth of the cells.

Table II also presents in condensed form the exact data upon which are based my statements to the effect that the persistence of the circle and the presence of the zigzag arrangement are normal features of the heterotypic metaphase in this species. These state-

TABLE II

SURVEY OF CELLS IN HETEROTYPIC METAPHASE IN OENOTHERA MURICATA

NUMBER OF CHROMOSOMES CLEARLY ATTACHED END TO END, AND NATURE OF ATTACHMENT		NUMBER OF CELLS	
A. All chromosomes visible			
Circle of 14, complete and regularly zigzag		34	
Chain of 14, complete and regularly zigzag		10	
	Total		44
Circle of 14, complete, with irregularity in arrangement		8	
Chain of 14, complete, with irregularity in arrangement		6	
	Total		14
			58
B. Some of circle obscure, but all visible chromosomes showing regular zigzag arrangement			
All visible chromosomes in one series			
	Chromosomes		
	13	1	
	12	17	
	11	11	
	10	20	
	9	24	
	8	18	
	7	19	
	6	26	
	5	14	
Visible chromosomes in more than one series, separated by obscure chromosomes			
	Chromosomes		
	8 and 4	2	
	8 and 3	1	
	7 and 3	2	
	6 and 5	3	
	6 and 4	4	
	6 and 3	3	
	5 and 5	2	
	5 and 4	4	
	5 and 3	4	
	4 and 4	3	
	4 and 3	6	
	4, 4, and 4	1	
	Total		185

TABLE II—*Continued*

NUMBER OF CHROMOSOMES CLEARLY ATTACHED END TO END, AND NATURE OF ATTACHMENT	NUMBER OF CELLS
C. Some of circle obscure, but irregularity visible in zigzag arrangement	
Visible chromosomes	
13	1
12	6
11	2
10	8
9	5
8	4
7	6
6	4
5	3
7 and 4	1
6 and 3	1
5 and 4	1
5 and 3	2
4 and 4	2
Total	46

ments seem to be justified in view of the fact that in practically one-fifth of the cells it has been possible to trace out the entire circle or chain, and in most of the other cells a majority of the chromosomes has been visible and their arrangement in metaphase in conformity with the rule suggested.

The circle remains intact until anaphase, at which time adjacent chromosomes are pulled to opposite poles. The V-shaped chromosomes keep together as they pass to the poles, so that one practically never sees a lagging one. Very rarely, some evidence of a longitudinal split may be observed as the chromosomes near the poles. As a rule, however, this does not appear until later. The daughter nuclei are constituted after the manner typical of *Oenothera*. When the normal number of chromosomes is involved, one tends to occupy the center, with the others around the periphery of the nucleus (fig. 20). For a time they may be slightly attached, but after the nuclear membrane has been formed, the attachment is quickly lost because a period of growth ensues, the nucleus becoming much larger and the chromosomes consequently more widely separated. The chromosomes also expand at the same time, although to a lesser degree than the nucleus as a whole. The ends of the chromosomes elon-

gate, and it is at this point that it is generally seen for the first time that they have undergone a longitudinal split (fig. 21). As elongation proceeds, the ends of the split halves diverge, so that the whole chromosome comes shortly to resemble a Maltese cross. In mid-interkinesis the time of maximum expansion is reached (figs. 22–24). The chromosomes are in general X-shaped. They have swollen tips and centers, and sometimes there seems to be another swollen portion midway between end and center, although this cannot always be seen.

One or more spherical nucleoli make their appearance in early interkinesis (figs. 22, 23). They are in contact with the chromosomes, remain small and colorless, and disappear before the nuclei disorganize. Their relation to the chromosomes strongly suggests that they originate from these, and hence arise *de novo*.

Very little need be said about the remaining stages, which differ in no way from corresponding stages in the other species of *Oenothera* examined. Chromosomes and nuclei pass through a period of contraction, the X-shape being retained until after the disappearance of the membranes. Multipolar spindles give place to bipolar ones, and the chromosomes are gathered in a regular manner to the plates. The two figures are constituted simultaneously, the angle which they bear to each other varying (fig. 25). As seen from the side in metaphase, each chromosome is distinctly a double affair, and in turn the halves are often constricted to some extent at the center. Anaphases are normal, and the granddaughter nuclei are formed as were the daughter nuclei. At first the chromosomes are distinct and separate (fig. 26), but a process of elongation occurs as the nuclei increase in size and delicate threads are sent out from the various chromosomes, uniting to form a loose and delicate reticulum (figs. 27, 28). A passage of stainable material from the chromosomes into these threads finally results in an irregular network, and the loss of visible individuality on the part of the chromosomes.

The four spores are formed simultaneously by a process of invagination of the cytoplasm from without inward, along the lines of the future cleavage. These do not seem to penetrate to the center, however, but delicate cleavage planes appear, completing the separation. This is particularly interesting in view of the absence of cell

plates and the early disappearance of interzonal fibers after the homotypic divisions.

Discussion

O. muricata is probably the most striking species yet examined, so far as its cytology is concerned. It shares with *O. biennis* and *O. biennis sulfurea* the distinction of having no pairing whatever of homologues in the late heterotypic prophase; but in the fact that all fourteen chromosomes are found in the same circle, this species represents the extreme limit to which the development of circles can attain. One cannot help feeling that a chromosome behavior so unusual must be full of significance, especially as *Oenothera* is unique from the genetical standpoint also. I have discussed previously in some detail what seems to me to be the probable significance of the phenomena observed (**6**). A brief review of some of the principal points, however, may not be out of the way in connection with this study of *muricata*.

In the first place, it is quite certain that the chromosomes are not arranged hit or miss within the circle. They must be so placed that the method of distribution to the poles in the heterotypic anaphase will ordinarily result in the separation of the members of each pair of homologues; otherwise non-disjunction would be the result in an impossibly large number of cases. It is possible to calculate what the chances of a distribution free from non-disjunction will be in a circle of fourteen, provided the chromosomes are placed entirely according to chance, remembering that the members of a pair of homologues will be separated in the reduction division (with every second chromosome going to the same pole) only when they are adjacent in the circle, or separated from each other by intervals of two, four, or six places. The total number of ways in which the fourteen chromosomes, acting as units, can be arranged within a circle of fourteen is 13, and the number of arrangements that will result in the separation of the members of every pair of chromosomes, and complete freedom from non-disjunction, will be 7. 6. The ratio of these is 1716:1. Only one cell out of 1717, on the average, will be entirely free from non-disjunction if the chromosomes are arranged merely by chance within the circle. There is,

however, no evidence of any such enormous prevalence of non-disjunction in *O. muricata* or any other species of *Oenothera*. We are forced, therefore, to abandon the idea that the position of the chromosomes in the circle is a mere matter of chance. On the other hand, if it be true that each pair of homologous chromosomes is definitely placed within the circle, then it is most likely that the same applies to each univalent chromosome also, and that each has its own place in relation to the other chromosomes; and the circle, which seems to be uniformly present throughout the species, is uniformly constructed as well.

Coupled with this is the clearly observed fact of the zigzag arrangement in the heterotypic metaphase, and the regular passage of every second chromosome to the same pole. If the chromosomes are arranged according to a set scheme within the circle in all cells, then such a distribution can have but one result. It is obvious that in every cell in which the zigzag arrangement is found to be wholly regular, the same chromosomes will proceed together to the same pole. Those passing to one pole are therefore as much linked, so far as the genetical effect produced is concerned, as though they were all a part of one chromosome. Hence we may say that the circle as a whole acts like one large chromosome pair, the members of which, each consisting of seven chromosomes, are separated to opposite poles. If a large amount of heterozygosity exists within the circle, as I believe is the case, the complexes resulting from the heterotypic division will differ in certain respects. As there are but two kinds of complex, there can be only two possible sorts of gamete. Owing probably to the presence of a balanced lethal situation, only the combination of the two complexes can survive, and so the species will breed true in the main. This seems to be the most obvious explanation of the relation between the undoubtedly unique chromosome behavior and the equally peculiar genetical phenomena, not alone in *muricata*, but also in various of the other species of *Oenothera*.

Irregularities in the zigzag arrangement, if the situation is as described, will alter the normal genetical result wherever they occur. In some cases they will lead to an abnormal numerical distribution, eight chromosomes passing into one cell and six into the

other. Sperms containing eight chromosomes may be capable of functioning and giving rise to fifteen chromosome individuals, although I am not acquainted with any evidence for the existence of fifteen chromosome plants in selfed lines of *muricata*. As for those possessing but six chromosomes, it is probable, judging from the entire lack of reported thirteen chromosome evening primroses, that in all cases they will be unable to function.

Irregularities in metaphase, however, do not necessarily lead to disturbance in the number of chromosomes distributed. In many cases the number passing to the poles will be normal, but both members of one of the pairs of homologous chromosomes will pass to the same pole, with the consequent absence of either member of some other pair in the resultant cell (**6**). Such cells, lacking entirely a representative of one of the pairs, will probably fail to develop functional sperms.

Other cells, as I have brought out in detail in connection with *O. biennis* and *O. biennis sulfurea*, will not only have the normal number of chromosomes, but a representative of every pair of homologues as well; but because of the irregularity in the zigzag arrangement, one or more chromosomes normally belonging to one complex will be found to have exchanged places with their homologues, and so be situated in the other complex. I have previously referred to this under the name of "interchromosomal crossing over." The resultant complexes, possessing a complete set of chromosomes, in most cases at least should prove functional, but the genetical result of this exchange ought theoretically to be of considerable importance.

In crosses, plants resulting from the union of sperms containing such complexes with normal eggs should develop into cross-overs. In selfed lines new characters should appear, and others that are normally present should fail to appear, for individuals arising from the union of such irregular complexes with the normal type would as a result have one or more pairs of identical chromosomes, depending upon the number exchanged. To illustrate, if we represent one complex by the letters ABCDEFG and the other as A′B′C′D′E′F′G′; and if, as a result of irregular distribution, A and A′ are exchanged in a certain cell, a plant arising from the union of a sperm having the

complex A′BCDEFG with the normal A′–G′ would have two A′ chromosomes, but no A. It being a selfed line, the two A′ chromosomes would probably be identical. Dominant characters depending upon the presence of genes in A would be lacking, and recessive characters depending upon genes in A′, and which had never before been visible because of the enforced heterozygosity of the species, could now express themselves. In cases where the exchange affects a single chromosome pair only, the difference between the resultant individual and those arising normally might be very slight. Where the number involved is greater, however, the effect should be more striking.

I wish at this time to emphasize the tentative nature of these suggestions. There is no question in regard to the cytological facts. They are clearly observed and easily demonstrable, but it is possible that the attempt to apply these phenomena to the genetical situation has not been entirely in keeping with the facts as they will in time be revealed. In the light of present knowledge, however, they seem to point the way toward a solution, based upon chromosome behavior, of many of the problems presented by the genetical behavior of *Oenothera*. It is hoped that they will at least serve to stimulate research in this direction, and that cytological investigation will develop many concrete data upon which to base further research. It is hardly necessary to suggest the desirability of *Oenothera* geneticists knowing so far as possible the chromosome arrangement and behavior in meiosis in the case of every plant used in breeding work.

Summary

1. Early stages in the heterotypic prophase in every way resemble those found in previously described species. They give evidence of the presence of telosynapsis as opposed to parasynapsis.

2. The stage known in most plants as diakinesis is absent in this species. There is no pairing of homologous chromosomes, but instead all of the fourteen univalent chromosomes are found to be united end to end to form a large closed circle, or occasionally an open chain. This configuration appears to be normally present and typical of the species.

3. The circle remains intact throughout the heterotypic meta-

phase, and spindle fiber attachments are made in such a way that adjacent chromosomes are pulled toward opposite poles. In general, the position of the circle in the spindle is horizontal, but since the chromosomes are alternately pulled to upper and lower poles, it takes on a regular zigzag appearance as seen from the side.

4. Irregularities occur in the zigzag arrangement in approximately 20 per cent of the cells.

5. The circle breaks up with the pulling apart of the chromosomes in anaphase. Subsequent stages in every respect are like those previously described for other species.

6. The chromosomes are without much doubt arranged within the circle according to a fixed scheme, for otherwise a certain amount of non-disjunction would occur almost every time that a reduction division took place.

7. If it be true that the chromosomes are arranged in a definite fashion within the circle in all cells, then it naturally follows that as a result of the normal separation of adjacent chromosomes in heterotypic anaphase the same chromosome complexes will in every case be formed at the poles.

8. There will then be but two kinds of complex formed, and two kinds of gamete; and the presence of balanced lethals probably accounts for the fact that neither can function in the homozygous condition, but only a combination of the two can be successful.

9. Irregularities in the zigzag arrangement doubtless lead to abnormal distribution of the chromosomes, which may result in functionless spores or gametes when the resultant complexes lack a representative of one or more of the chromosome pairs; but in many cases irregularities merely cause an exchange of the members of one or more homologous pairs from one complex to the other, and the complexes thus formed being complete, the cells containing them may be capable of functioning.

10. Such complexes, although complete, are abnormal. If they function in crosses with other species, they may result in the appearance of cross-over individuals. In selfed lines the union of such complexes with normal ones containing the proper lethal may result in a plant deviating more or less from the usual type.

In conclusion, I wish to thank Professor B. M. DAVIS for allow-

ing me to collect material from his cultures, and for many expressions of interest in the work. Grateful acknowledgment is also made to the officers of the Marine Biological Laboratory, Woods Hole, Massachusetts, especially to Professor I. F. LEWIS, for facilities placed at my disposal during several successive summers.

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EXPLANATION OF PLATES III, IV

Figures were drawn with the aid of a camera lucida, using a Spencer compound binocular microscope, and a Bausch and Lomb 1–12 apochromatic objective with 25× compensating oculars. They have been reduced one-fourth in reproduction. Present magnification approximately 2800 diameters.

PLATE III

FIG. 1.—Hollow spireme; threads unsplit.

FIG. 2.—Early second contraction, showing growing condensation in middle of nucleus and peripheral loops.

FIGS. 3–5.—Late second contraction stages.

FIGS. 6–10.—Circle of fourteen chromosomes in late prophase, corresponding to period generally called diakinesis.

FIGS. 11, 12.—Circle broken open and resulting in chain of fourteen chromosomes; late prophase.

PLATE IV

FIG. 13.—Multipolar spindle; circle of fourteen chromosomes still intact.

FIGS. 14–16.—Heterotypic metaphase with circle of fourteen chromosomes; adjacent chromosomes ready to pass to opposite poles, giving zigzag appearance (spindle omitted in figs. 14 and 15).

FIG. 17.—Chain of fourteen chromosomes in heterotypic metaphase, regularly zigzag (spindle omitted).

FIG. 18.—Irregularity in zigzag arrangement in heterotypic metaphase (spindle omitted); two adjacent chromosomes at left end ready to proceed together to upper pole, and another pair at right end about to pass to lower pole.

FIG. 19.—Another irregularity in a chain of fourteen chromosomes; two at different points suspended in center of spindle without visible fiber attachment.

FIG. 20.—Early telophase; chromosomes gathered at pole and attached, but nuclear membrane as yet unformed.

FIG. 21.—Early interkinesis; chromosomes beginning to take X-form.

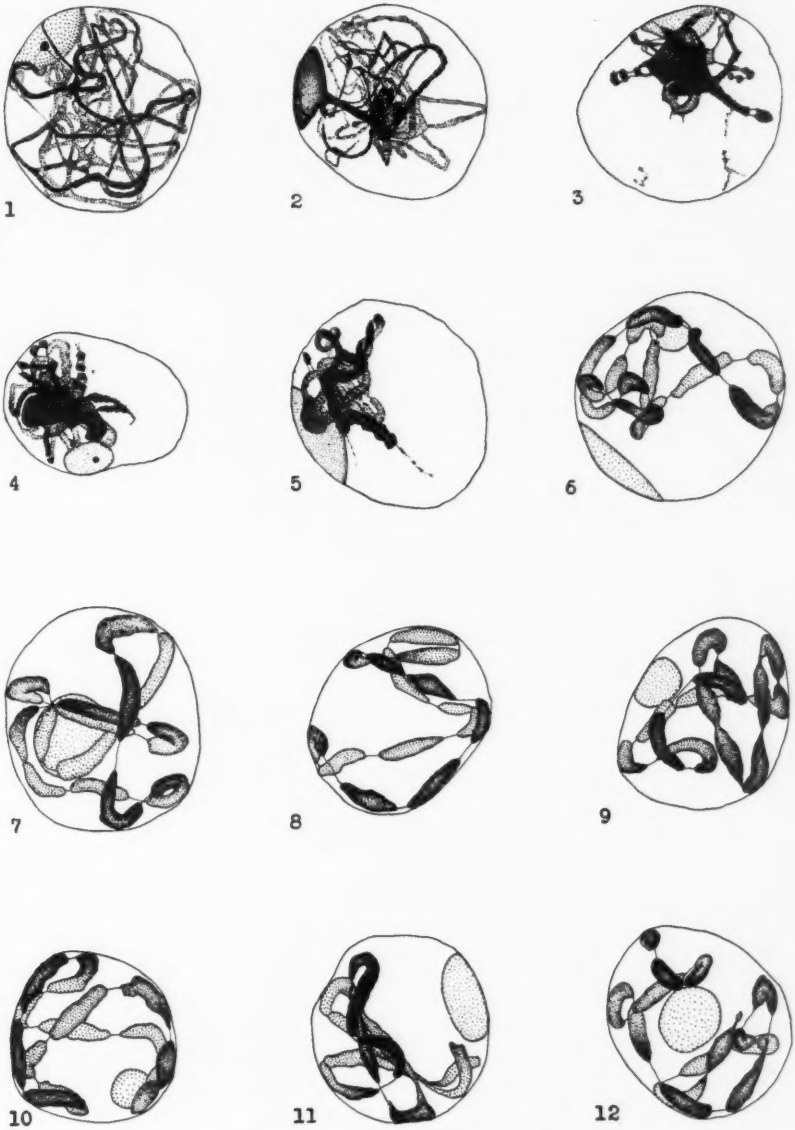
FIGS. 22, 23.—Mid-interkinesis.

FIG. 24.—Mid-interkinesis; both nuclei in one pollen mother cell; six chromosomes in one nucleus and eight in other.

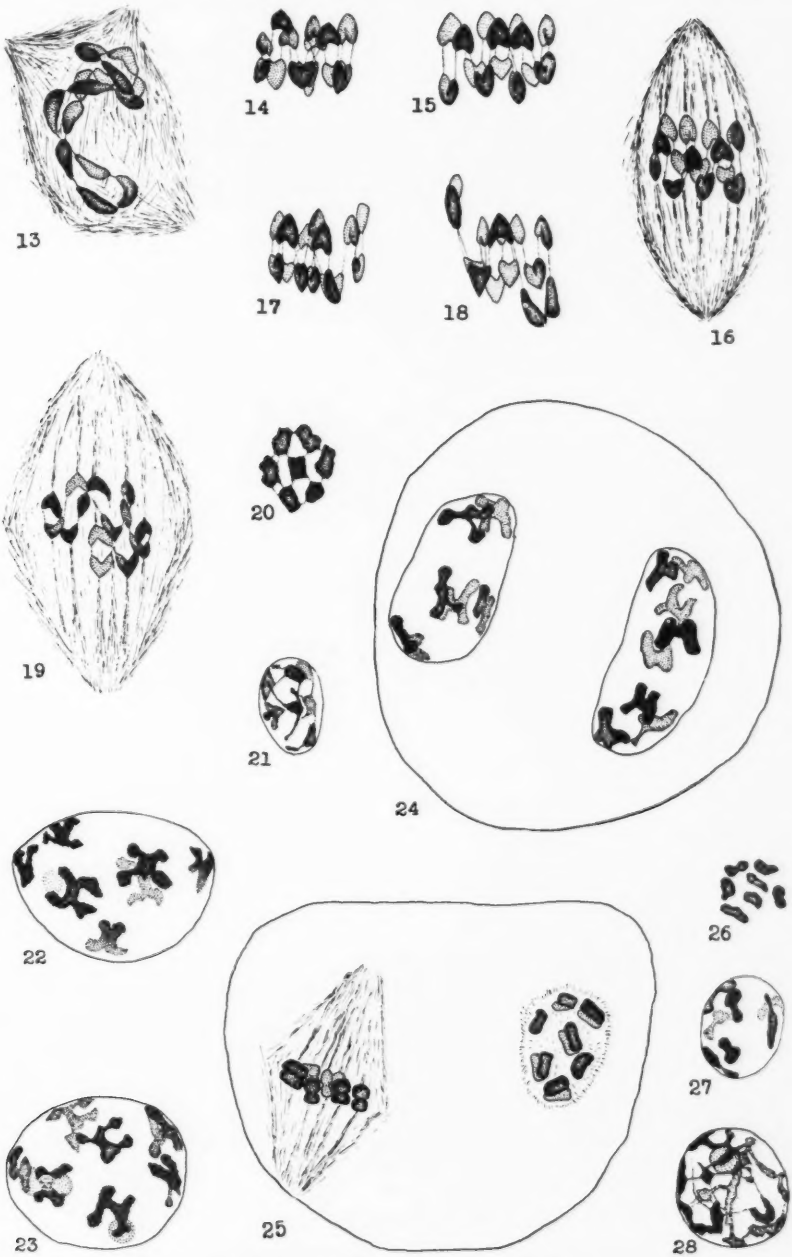
FIG. 25.—Homotypic metaphase, side view of one plate, polar view of other.

FIG. 26.—Second telophase.

FIGS. 27, 28.—Passage of granddaughter nucleus into resting condition; individuality of chromosomes lost sight of in fig. 28.



CLELAND on OENOTHERA MURICATA



CLELAND on OENOTHERA MURICATA

ORGANIZATION AND SIGNIFICANCE OF LENTICELS IN DICOTYLEDONS

I. LENTICELS IN RELATION TO AGGREGATE AND COMPOUND STORAGE RAYS IN WOODY STEMS. LENTICELS AND ROOTS.[1]

RALPH H. WETMORE

(WITH PLATES V, VI)

Introduction

In a recent joint article by Professor JEFFREY and the writer,[2] on the morphological and evolutionary significance of the parichnos, it was pointed out that this structure was probably widespread as an organ of aeration in ancient arboreal forms. This belief is supported by the general existence of a parichnos in the Lepidodendraceae accompanying each foliar trace into the leaf, and there becoming confluent with the intercellular spaces of the mesophyll. A reason for the presence of such an aerating channel was found in the absence of cauline stomata. Also the retention of the paired parichnos scars was explained as permanent aerating structures after the fall of the leaves. These paired structures have indeed been considered as primitive lenticels (POTONIÉ **10, 11**; SCOTT **14, 15**). It was pointed out as further evidence of the general distribution of the parichnos in ancient forms, that there are devices initially present in certain conifers and in *Ginkgo biloba*, as well as in certain species of *Equisetum* (JEFFREY **5**), which were clearly parichnos-like in nature. In the conifers and *Ginkgo* the exact conditions of the Lepidodendraceae are duplicated, both with regard to the actual form and position of the parichnos, and the general absence of cauline stomata.[3] In these forms the parichnos is but transitory, soon being lost because of the increased diameter of the stele, but to supporters of the bio-

[1] Contribution from the Laboratories of Plant Morphology, Harvard University.

[2] Unpublished. Ann. Botany.

[3] Cauline stomata were found only on the decurrent leaf bases of *Taxus canadensis* and *T. cuspidata*.

genetic law its initial presence indicates the existence of a parichnos as a permanent structure in the ancestors of the conifers and *Ginkgo*, as well as of the Equisetaceae. Unfortunately, there is at present inadequate fossil material to prove this fact conclusively. It is significant also that the primary lenticels on the stems of the conifers invariably appear with the fall of the leaves, as paired structures on either side of the foliar bundle scar, just as in the Lepidodendraceae. This fact is true even in those conifers when the parichnos is no longer present. Moreover, such a condition is the permanent one in coniferous roots.

Since the parichnos is present in only a few genera of conifers, and in these early becomes an obsolete structure, aeration must be furthered by other means. The primitive lenticels, therefore, early acquire secondary relations and connections, and in this readjustment they become transversely elongated, thus enabling them to aerate the maximum number of vertically short rays and thence the other parenchymatous tissue of the stele. Furthermore, it is of interest that other lenticels of haphazard distribution later appear on coniferous stems, thus providing air for the ever enlarging stele with its continually increasing number of wood rays. With these ideas in mind, attention is directed to the angiosperms.

Materials and methods

The results of this research are based on a study of some 279 species and 35 varieties of dicotyledons, representing 89 genera of 35 families, and comprising both exotic and indigenous forms. Data were assembled from all these forms, entailing a study of the lenticular organs of both stem and root. Not only was information gathered on the size, shape, type, and distribution of these organs, but material was also collected for laboratory investigation.

With the material of both stems and roots, pieces of various ages were obtained. These specimens were blocked up in small segments, averaging 1 cm. long, and preserved in 70 per cent alcohol. When used, the material was halved, one portion being softened, imbedded, sectioned, and stained after the generally accepted methods employed for ligneous structures (JEFFREY 6). The second portion was treated for removal of epidermis and periderm. This meth-

od is an unpublished one, devised by JEFFREY for this purpose, and is especially applicable in investigating the presence or absence of stomata. It consists essentially of subjecting the material to the action of a diluted saturated solution of sodium chlorate in hydrofluoric acid. The strength of the solution used is determined by the material to be macerated, and is ascertained by experience alone. It should not be used pure for this work, but according to demand. The stock solution is prepared by adding sodium chlorate crystals to concentrated hydrofluoric acid until there is a surplus of crystals present. A wax covered bottle is necessary as a container for this solution. When material is to be macerated, this also must be placed in wax covered bottles, which must be clean, and free from foreign liquids as well as solids. If not thoroughly devoid of extraneous matter, rapid oxidation ensues on addition of the maceration fluid, usually with the production of sufficient heat to melt the wax. This means that the glass is exposed to the vigorous attack of the acid and the material is thus frequently lost. After the material to be treated for removal of periderm or epidermis is placed in the bottles, a small amount of water is added. The maceration fluid is then poured on to a desired strength, varying from about 20 to 60 per cent, according to the age of the twigs and the nature of the periderm. Young material for epidermal removal requires a weaker solution, whereas older material with a heavy periderm necessitates a more concentrated reagent.

After a few days in this fluid, the time being a variable factor, the material is washed thoroughly under running water. It is then found that the cork cambial or subepidermal cells have been macerated to a degree permitting the removal of the periderm or epidermis. If these sections are then shaken vigorously in water, to remove adhering bits of cortex or phelloderm, they are ready for bleaching. This procedure is a replica of the last, the same reagent being used as for maceration, only in weaker solution, 10–20 per cent being of adequate strength. Careful watching of the material for a day or two shows that it has become absolutely white. After again thoroughly ridding the material of all bleaching fluid under running water, it is ready for staining. As a result of several trials, the iron-alum haematoxylin of HAIDENHAIN proved the most satisfactory

stain, when used in small quantities over long intervals of time. A counter stain, however, was found to be of little additional value. After staining, the sections, whether epidermal or peridermal, were then dehydrated, cleared in benzol, and mounted in balsam according to the usual methods.

This procedure was used for removal and study of the epidermis and the periderm of many different species of conifers and angiosperms. It made possible the decision as to whether stomata were present or absent, whether lenticels first appeared over these or not, and the nature of the lenticels themselves.

Angiosperms

In the angiosperms anatomical conditions are very different from those found in even the highest conifers. In no case are there indications of such an ancient structure as the parichnos, even in the most conservative organs. Such a structure is not a requisite to survival because of the general existence of stomata on the stems of angiosperms.[4] Because of these organs, the epidermis is viable to gases, and aeration is thus made possible until the formation of periderm is initiated. Very probably the parichnos and generally distributed cauline stomata have never been correlated structures at any time in plant evolution. STAHL (16) differentiated lenticels as found in angiosperms into those of primary or secondary nature. The former, he claimed, originated under stomata, as previously stated by UNGER (19) (although he later seemingly discarded this belief) and TRÉCUL (18). Later workers all agree on this point.

Since the cauline lenticular structures of the angiosperms are primarily substomatal in origin, their distribution is haphazard and at first entirely without internal correlations. Their appearance, as STAHL showed, is usually followed promptly by the origin of the initial peridermic sheath. He pointed out, however, that in cases where an abnormally heavy cuticle exists, the primary periderm

[4] DEVAUX (3) mentions eight species, widely separated in affinity, in which he failed to discover stomata. In no instance has the writer found them absent in the material collected for this research, although none of the forms named by DEVAUX was contained therein. It is worthy of note that the same investigator found cauline stomata invariably much larger, although fewer in number, than those on the leaves of the same species.

may never develop at all. The writer found several instances of this condition.

This primary periderm may be one of lasting nature, and even a permanent structure, although most frequently it is quickly replaced as a result of secondary phellogenic activities within. If the initial sheath is persistent, the lenticels of stomatal origin will also become lasting structures. It is common, however, for them to lose their initial limitation to the region of the substomatal cavity, and to become greatly increased in size, with other relationships than earlier shown. Thus primary structures may remain as such, or they may assume secondary proportions and connections. *Betula* is typical of this interesting situation. STAHL (**16**) asserted that he could not find a single cauline stoma in strips of young birch bark that had not given rise to a lenticel. It is worthy of note that, despite their substomatal origin and their persistence as primary structures, they early cease to be limited by stomatal confines and become extended transversely, so that on older trees they appear frequently as horizontal markings continuing around a large portion of the circumference.

The secondary relationships acquired by these lenticels are equally significant and exactly comparable with those possessed by the secondary structures which arise with the appearance of other periderm formations than the initial one. DEVAUX (**3**) stated that although primary lenticels showed definite relationships to stomata, those of secondary origin seemed devoid of any such connection. It is true that externally, as he viewed them, there is none apparent. Internally it will be shown that all lenticels of secondary relationship, whether of primary or secondary derivation, display the most intimate correlation with the storage rays, irrespective of the type and distribution of the latter.

The writer finds that secondarily modified, primary lenticels, and all secondary lenticels are capable of classification according to shape. There are those which are oriented transversely. These *transverse* lenticels, as the writer has labeled them, are more characteristic of the members of the lower angiospermous affinities, and the (generally conceded) less highly evolved genera of the higher families. Such exists in *Betula alba* var. *papyrifera* (fig. 1). The remain-

ing lenticel bearing forms, chiefly belonging to higher groups in the systematic scale, and the probable more highly evolved genera of the lower assemblages, possess what the writer calls *longitudinal* lenticels. These have the fissure elongated in the direction of axis. Exemplifying the latter is *Alnus rugosa* (fig. 4). At this point it will be well to mention that both of these types of lenticels have been referred to by different writers, but no significance was attached thereto. Many writers considered all mature lenticular structures extended crosswise, as is apparent from the works of DE CANDOLLE (2), MOHL (9), MEYEN (8), SCHACHT (13), SACHS (12), and others. Longitudinal orientations have seldom been noticed, although STAHL (16), WEISS (20), and DEVAUX (3) do mention them in specific instances. Certain of the earlier writers, as MOHL and MEYEN, did call attention to lenticels being longitudinal first and then transverse. These references undoubtedly were to primary lenticels, which early are always of this orientation, due to the elongation of the stomata from which they were derived. They may remain so or become transverse with maturity.

The classification of lenticels proposed by the present writer is not opposed to that of STAHL (16) nor to the modification suggested by DEVAUX (3). It is a result of another method of approach to the problem, as well as of the employment of very different criteria. That the two systems are not coincident will be apparent when it is mentioned that the writer finds both types of STAHL's lenticels in each of the transverse and longitudinal classes suggested herein. This will be evident as the various illustrations used in the work are referred to. The grouping as used in this research is intended to be suggestive of internal relationships which will be shown to exist between the lenticels and the storage rays within. The earlier types were based on the existence of lenticular structures as superficial organs, devoid of any internal connection. The illustrations in the sequel will make this point clear. Fig. 13 is a representation of a lenticel of *Alnus rugosa*, an example of STAHL'S type I. The banded nature of the structure is clearly visible. A further example of this type is indicated in fig. 2, a lenticel of *Betula populifolia*. This differs from the last in remaining long closed, so far as ruptures in the clos-

ing layers are concerned. In *Alnus rugosa* only the inner three or four of these lamellations remain unbroken. In contrast to these two examples there are shown in fig. 14 two lenticels of the root of *Sambucus canadensis*. Although under low magnification, they can be seen to be of STAHL'S type II, since the complementary tissue is clearly not lamellate, the cells appearing practically uniform in size.

That these earlier groupings were not as fundamental as supposed is suggested by KLEBAHN'S (7) discovery of lenticels which did not conform to the limitations of either of STAHL'S groups, but rather seemed between the two. Also, DEVAUX'S experimental studies pointed to the same conclusion, when he found that by altering the humidity of the medium he could change the type of lenticel at will. These types are of some significance however. As KLEBAHN has pointed out, STAHL'S first type is undoubtedly a more efficient protective organ than his second, and indicates a higher evolutionary status. The writer finds that the major part of the cauline lenticels studied in this research belong to this higher class, the second type (the diffuse lenticel) being the exception rather than the rule. In roots, only those of STAHL'S second type have been found, possibly due to the conservative nature of this organ, or possibly, as asserted by DEVAUX, to the presence of moisture in the soil.

In discussing these modified primary and secondary cauline lenticels, since they show a close relationship to the rays within, they will be treated along with the form of storage ray present, whether aggregate, diffuse, or compound. Under the different types will be mentioned examples of both transverse and longitudinal types of lenticels, with an endeavor to point out internal anatomical reasons for the nature of the lenticel thereon occurring.

For the sake of convenience in designating the types of rays concerned, the terminology of JEFFREY (6) has been adopted. Storage structures composed of aggregations of uniseriate rays or multiseriate rays of small dimension, in close proximity to each other, have been termed "aggregate." Such congeries of small rays extend for considerable distances vertically in the stem. Exemplifying this condition are many of the generally conceded lower angiosperms, for example, *Alnus incana* (fig. 10) and *A. japonica* (fig. 9). If, however, instead of the composite aggregation of small rays and fibers,

the storage structure appears as a homogeneous band of parenchymatous tissue, the ray is termed "compound." Such compound rays, rare in arboreal and fruticose forms, are found in at least the mature stems of *Quercus*, where they are greatly elongated vertically. Fig. 11 represents a transverse view of a small stem of *Quercus alba*, where a compound ray is shown. In general, however, the initial aggregations in woody angiosperms become diffused into multiseriate structures of varying width and height, more or less uniformly distributed throughout the stem. Such storage structures are spoken of as "diffuse" rays. The more primitive forms possessing diffuse rays tend to have the consequent multiseriate components vertically shorter than those in higher systematic groups.

In the present paper, cauline lenticels and their relationships will be discussed in species with aggregate or compound rays. A study of the lenticular situation in roots will also be reported. A later paper will complete the investigation with a summary of the situation in species possessing diffuse rays.

Lenticels and aggregate storage rays

The fact that there are definite internal conditions accompanying the presence of transverse lenticels, and that these conditions are materially different when longitudinal structures exist, can well be pointed out by reference to concrete examples.

In *Alnus* it is interesting that both types of lenticels exist in different species. Thus fig. 3 (left) illustrates the situation in *A. incana*. The lenticels here are clearly transverse as well as horizontally seriate. Fig. 3 (right) is a portion of a branch of *A. japonica*. The lenticels here are much as in the preceding species, although smaller and not horizontally seriate. In contrast to these two may be mentioned *A. rugosa*, two pieces of which are shown in fig. 4. Here is clearly indicated a longitudinal orientation in all the lenticular organs, although they exist in varying sizes. This difference in magnitude is a result of differential ages, such secondary lenticels increasing in number progressively with time.

It is instructive to compare internal conditions with these lenticular dispositions. Fig. 10 shows a transverse section of *Alnus incana*. Here four aggregate rays are clearly visible, and a fifth less

distinctly so. The lenticels, two in number, are also very apparent and close together. That an aggregate ray exists under each is noticeable, but it is equally noticeable that each lenticel not only subtends one of these, but many uniseriate structures as well. Such is the general situation in this species. Lenticels usually lie opposite one or more aggregate rays, but whatever co-ordination there exists between internal structures and lenticels is not a result of the influence of aggregate rays alone. An accompanying condition should be mentioned here. A short distance within the periderm the sclerotic pericycle is apparent, extending continuously across the field.

In *Alnus japonica* conditions are more or less the same, as shown in fig. 9. Here the single lenticel in the field is distinctly confronted by an aggregation of small rays; however, here again it is not confined in lateral extension to the limits of that ray, as it subtends several non-aggregated, uniseriate structures on either side as well. Here again also the sclerotic pericycle is continuous, being clearly visible between the outward ends of the rays and the periderm. In *A. rugosa*, as just mentioned, we find longitudinal lenticels. Here in cross-section (fig. 13) are portrayed two lenticels, each clearly subtending aggregations of rays. Moreover, in their vertical elongation these lenticels are much narrower, each more nearly corresponding to the width of an aggregate ray. It is also clear that the continuous pericycle of the other two species has now become thin and practically disrupted in places under the lenticels. Thus is assured a more direct communication between the lenticels and the rays, through the cortex.

To epitomize the situation as shown in the alders, it would seem that the primitive condition of relationship is found in *A. incana*. Here the lenticels are frequently in horizontal chains, related to uniseriate and aggregate rays alike. There seems to be no closer connection with the aggregations than with the more primitive structures, for the pericycle is uniformly heavy all the way around. In *A. japonica* another tendency becomes apparent. In spite of a great many series of sections having been cut, no case was found where a lenticel was not opposite an aggregate ray, although it is true that the lateral extension permitted it to confront those of uniseriate nature on either side as well. In this and the preceding spe-

cies, however, the pericycle remains continuous. Matters have progressed further in *A. rugosa*. Here the lenticels are clearly longitudinal, narrow in lateral extension, and unquestionably related to aggregate rays, and these alone. A few cases only were found where such lenticels were to any extent wider than the rays they subtend, but in every instance this larger lenticel was confronting two closely approximate aggregations. Moreover, the movement of gases in these regions between the lenticels and the rays is facilitated by the interruptions of the pericycle opposite the lenticels, although continuous elsewhere. Thus it seems that as the storage aggregation of rays has evolved, with its greater metabolic activities, there is an accompanying demand for an increased aeration of these structures to facilitate that accentuated metabolism.

These results are interesting also when the correlation is considered in relation to the extent of aggregation. *Alnus incana* is recognizably a primitive alder, with aggregations of uniseriate rays mostly, only occasional signs of their uniting to form multiseriations being visible (BAILEY 1, HOAR 4). On the other hand, HOAR shows that *A. japonica* has a higher aggregation, being largely composed of multiseriate units. *A. rugosa* is also of the latter type, with congeries of multiseriates for the greater part making up the storage ray. This correlation of internal ray structure, with the nature of the lenticels and distribution of the same, is most striking. In fig. 4 (right) is shown a section of a stem of *A. rugosa* in which rhytidome has appeared in the initial bark. At the base of the fissure, lenticels derived from the secondary periderm are apparent, clearly like their predecessors in orientation. It is significant that these are more or less in longitudinal rows. Investigation of such instances showed that they were lying along the aggregate ray which extends vertically for long distances in the stele. These vertical lines of lenticels are very apparent on older stems of *A. rugosa*, and are significant in this respect, since they still further increase the possibility of aeration of these storage organs.

Although *Alnus* alone has been treated thus far, similar conditions are found elsewhere. *Corylus*, also of the Betulaceae, is a very interesting genus. Fig. 8 shows a surface view of *C. americana*. Here the earlier secondary lenticels are clearly transverse. As the stem increases in diameter, however, many small longitudinal lenticels be-

come apparent, some even being found immediately on the already existing transverse lenticels. Although these are small, a careful examination of the figure will reveal their presence. Again internal studies appeared illuminating. The aggregate rays present are related to the transverse lenticels, as are those of *A. incana*, one lenticel often subtending several of these structures as well as a host of the uniseriate type. As these aggregations become more mature, and the components multiseriate, the longitudinal structures begin to appear. In no case was a lenticel of this type found otherwise than subtending an aggregate ray. Various species of *Corylus* showed this transitional condition. In *C. rostrata* the situation is the same, although the transverse lenticels are early replaced by longitudinal ones. *C. avellana* and *C. maxima* also duplicate these conditions.

Carpinus, of the same family, provides another case parallel to that in *Alnus*. *C. caroliniana* has broad, transverse lenticels, sometimes over aggregate rays, sometimes not. On the contrary, *C. japonica* has longitudinal lenticels distinctly opposite the aggregate rays, which are composed of multiseriate units.

These parallel instances serve to indicate that, with aggregate structures at least, there is a direct relation between the type of aerating device and the structure to be aerated. In general, the more highly evolved aggregate ray (that is, the one with multiseriate structures replacing those of uniseriate nature) has the more advanced type of lenticel, the longitudinal structure. With the localization of the lenticels in the region confronting the storage rays, the uniseriate structures lose their direct connection with the aerating devices. This is significant in the light of STRASBURGER'S (17) results. He found that in the majority of dicotyledonous trees and shrubs examined, these primitive rays were devoid of intercellular spaces. They were not starch bearing, and instead, like the erect cells of the multiseriate rays, were connected with the vessels by pits. He concluded that in these forms they served as adjusters of the sap flow in the plant, as did the erect cells already mentioned. This localizing of storage and aerating structures is accompanied usually by the thinning out of the pericycle, and even by its disorganization under the lenticels at least, thus still further accentuating the intimacy of lenticel and storage ray.

Lenticels and compound rays

In arboreal and shrubby forms the compound storage ray is only rarely met with. In the many forms examined, *Quercus* offers the only illustration. As with genera possessing aggregate rays, for example, *Alnus*, *Corylus*, *Carpinus*, it is interesting that there exist both transverse and longitudinal lenticels with the compound structures. These lenticels are small in the younger growths of *Quercus*, and as the bark is so heavy and cracked in older stems, it is difficult to find the structures at all; consequently, the investigation was mostly confined to comparatively young branches and stems. Since the lenticels are more or less insignificant, illustrations of the external views were omitted, being of little value in this connection; transverse sections, however, are shown. Fig. 12 is such a view of *Q. palustris*. The transverse lenticel is here clearly subtending a storage ray which even shows a definite curve toward the lenticel. Even at this magnification, it can be noticed that this ray was one of slow compounding. Several of those in the field are distinctly not homogeneous even in the cambial region of the wood, the light and dark rows of cells indicating the presence of both fibers and rays. The stem sectioned was nine years old, although but seven of the annual rings are visible in the photomicrograph. This means that here a nine-year old stem still has aggregate rays in process of slow compounding.

To contrast with the condition in *Q. palustris*, a corresponding section of *Q. alba* (fig. 11) is shown. Here the longitudinal lenticel, characteristic of this species, is over a curving ray as before. Although the figure does not show the inner annual rings, it may be mentioned that the time for passing through the aggregate stage to that of the fully compound ray required less than one year; in other words, the storage ray was of a much higher type, reaching its mature condition within the first annual ring. This implies a more highly evolved anatomical situation, and the fact that the elaborate storage device occurs early would necessarily mean that the structure was many times more efficient. Its metabolic activity would be greatly magnified, and this would necessitate increased respiration. The air for this purpose could most efficiently be supplied by the longitudinal lenticel. Early in the formation of rhytidome, before

the bark is so badly ridged and cracked as to make it unrecognizable, conditions such as are shown in fig. 5 are frequently found. This is an example from *Q. rubra*, which has longitudinal lenticels. Its compound rays become fully developed within the first three or four years in the specimens studied. Here vertical rows of longitudinal lenticels are clearly indicated, so much so in places that they almost resemble one greatly elongated lenticel in the proximity of the individual components. With such aerating devices as these, it is clear that the compound ray would be much more efficiently supplied than by transverse lenticels.

Although but three species have been mentioned, they are illustrative of the conditions found in the genus. Like *Quercus palustris* were found to be *Q. velutina* and *Q. coccinea*. Like *Q. alba* and *Q. rubra* were *Q. ellipsoidalis*, *Q. stellata*, *Q. macrocarpa*, and *Q. Saulii*. Thus a study of the oaks seems to indicate that the type of lenticel is not correlated with the systematic grouping of the oaks into white and black subdivisions, but one which rather implies definite anatomical differences in evolution. The lower types of storage rays, becoming compound after many years in the more primitive aggregate condition, have accompanying them the more primitive types of lenticels. In contrast, irrespective of systematic grouping, those species which quickly reach the more highly evolved and more efficient storage ray acquire the longitudinal lenticel. They also tend to become very numerous along the vertical extension of these storage rays, until longitudinal lines of them are found subtending the ray. Moreover, these longitudinal lines of lenticels may even result in fusions, until the individual lenticular fissures become continuous, giving a pseudolenticel sometimes over an inch in length.

The fact that these lenticels, irrespective of type, are invariably correlated with the rays to such an extent that the ray is still confronted by the lenticel, even when somewhat changed in its direction by growth, is difficult of interpretation unless construed in terms of gas exchange and respiration.

Roots of angiosperms

The study of the lenticels on the roots of dicotyledons shows surprising, yet not unexpected conditions. In the case of the stems,

the lenticels indicate an evolution directly parallel to the internal anatomical progress. This is not so with roots, however.

In so far as distribution is concerned, STAHL demonstrated that if lenticels were found on stems of a species, they also existed on the roots. DEVAUX agreed with this essentially, but went further, reporting them on some roots where they did not occur on stems, for example, certain herbaceous forms. The latter carefully studied the distribution of radical lenticels. In general, he found them located in pairs, one on either side of each rootlet. He proved this to be practically a universal situation, and referred to these lenticels as "basoradicellaires." He states: "Niveau d' insertion des radicelles semble être un lieu d' élection spéciale pour les lenticelles de la racine." This situation the writer is able to confirm. It should be added also that they are elongated transversely. In no case of roots examined have these paired appendage lenticels been entirely absent. However, two tendencies exist which make interpretation difficult at times. There is a well known tendency for the early abortion of rootlets. In consequence, many pairs of lenticels occur with no rootlet between. When sectioned in such regions, however, in every case examined they were in the position of a rootlet trace, that is, opposite a protoxylem point. Also, lenticels in many cases abort early. Rootlets are frequently found with but one or no lenticels accompanying them. A study of younger roots nevertheless shows them to be present initially, but often they are soon lost. DEVAUX mentions these abortions, saying that they are more frequent when rootlets are crowded.

The existence of these paired lenticels is well shown in fig. 7, which is a portion of a root of *Fraxinus nigra*. At the top is a rootlet with a transverse lenticel unmistakably present on either side; at the bottom another rootlet is seen. Only one side of the lenticel appears, but on that are two transverse lenticels, side by side. Several of these structures may occur on each side of a rootlet; they get progressively smaller, however, as one gets away from the base of the appendage. This condition is a common one, especially on older roots. *Alnus incana* offers another good instance of this situation (fig. 6). At the lower right is a portion of a broken rootlet. Extending to the left from this is a chain of lenticels. To the right of

the appendage a similar condition exists, although not apparent in the illustration. In the upper part a rootlet is seen with a single lenticel visible on one side, the other again not being visible. Other instances of paired lenticels with rootlet scars between can be detected on the segment.

Many such instances might be given, for any one root is as good as another. However, these two will suffice for external views, for transverse sections are equally as instructive in this connection. Fig. 14 is a section of the root of *Sambucus canadensis*. The rootlet has just left the root; on either side is a prominent lenticel. These cases might be multiplied indefinitely, but little is to be gained thereby, since the relationship is a universal one.

The situation as illustrated here is a significant one. The similarity of the arrangement of these lenticels to the primitive condition in the stems of conifers, and the permanent condition for roots in the same group are impressive.[5] In other words, the condition for roots at all times is that which is primitive for both stems and roots of conifers, and which is never found in angiospermous stems at any time. When this is placed along with the many other anatomical facts of equal import, one cannot with ease overlook the doctrine of the conservatism of root structures put forward by JEFFREY (**6**). Certainly it is true that the structure of the appendage rays in the roots does not warrant the lenticels being transverse at all times, and only related to the traces. In many cases the aggregate rays of the roots have considerable length, but in spite of this fact the lenticels are transverse. This is true in *Alnus japonica*. The aggregate appendage ray is present here, but the lenticels are still related to the rootlet, after the fashion found when but uniseriate storage structures were present, as in the conifers.

It will be remembered also that in the Coniferales cauline stomata were generally absent; this seemed to be a condition strictly accompanying the occurrence of the paired appendage lenticels. It is significant in this connection that roots are also devoid of stomatal organs, and they possess the same distribution of lenticels as in the conifers. In these two respects, therefore, the stems and roots in the conifers have their counterparts in roots of angiospermous affini-

[5] JEFFREY, E. C., and WETMORE, R. H., Ann. Botany (Unpublished).

ties. Furthermore, it will be remembered that on coniferous stems, secondary, diffuse, transverse lenticels occurred later, obscuring the primary relationship. In this connection, attention must be called to the existence of secondary transverse lenticels on the older roots of angiosperms as well. Since the radicular appendages occur in vertical lines, the paired lenticels must be likewise arranged. These diffuse lenticels can be found scattered in regions where no rootlets could exist. DEVAUX also reported these structures. Again we have a situation similar to that in coniferous stems, although there is a difference anatomically, as previously mentioned. The ray situation of angiospermous roots warrants a more highly evolved lenticular relationship than that most suitable to the uniseriate storage elements of the conifers, yet it does not exist. The conservatism of the root seems to offer the only logical explanation.

Summary

1. Lenticels may with advantage be considered *transverse* or *longitudinal*, in accordance with the orientation of the fissure.

2. The orientation of the cauline lenticel is clearly correlated with the nature of storage ray within.

3. Forms with aggregate storage rays of primitive nature in the stem, that is, composed largely of congeries of uniseriate rays, possess transverse lenticels. In contrast, these species in which the storage aggregations consist of multiseriate units, for the most part, are found to have longitudinal lenticels. In the latter cases the pericycle usually shows a disruption under the lenticular organs. *Alnus*, *Corylus*, and *Carpinus* typify this condition.

4. Forms with compound storage rays in the stem at maturity, but in which the compounding is completed only after many years, possess the more primitive lenticels, the transverse type. Those species in which the storage ray becomes compound within a very short time, one to three years, are found to have confronting each ray one or many longitudinal lenticels. These may even be so closely approximated as to appear as a single greatly elongated structure. *Quercus* offers the only example found of this situation.

5. Roots, irrespective of internal conditions and taxonomic affinities of the species concerned, all show paired appendage lenti-

cels, the primitive type found to be characteristic of young coniferous stems and all coniferous roots, indicating the conservative nature of the root.

6. The intimate relation between the type of storage ray and the form of lenticel facilitates a satisfactory aeration of the living tissues within the stele, with the consequent maximum metabolic activity.

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EXPLANATION OF PLATES V, VI

PLATE V

FIG. 1.—Portion of branch of *Betula alba* var. *papyrifera* with transverse lenticels; ×1.5.

FIG. 2.—Transverse section of transverse lenticel of *Betula populifolia;* ×12.

FIG. 3.—Portions of branches of *Alnus incana* (left) and *A. japonica* (right) with transverse lenticels; ×1.

FIG. 4.—Segments of stem of *Alnus rugosa* with longitudinal lenticels; ×1.

FIG. 5.—Segment of branch of *Quercus rubra* with elongated vertical lenticels; ×1.

FIG. 6.—Segment of root of *Alnus incana,* showing lenticels related to rootlets; ×1.

FIG. 7.—Segment of root of *Fraxinus nigra,* showing relation of lenticels to rootlets; ×1.

FIG. 8.—Segment of branch of *Corylus americana,* with small longitudinal lenticels appearing on transverse lenticels; ×1.

PLATE VI

FIG. 9.—Portion of transverse section of *Alnus japonica,* showing relation of transverse lenticels to both aggregate and uniseriate rays; ×10.

FIG. 10.—Portion of transverse section of *Alnus incana,* showing relation of lenticels to both aggregate and uniseriate rays; ×10.

FIG. 11.—Portion of transverse section of *Quercus alba,* showing relation of longitudinal lenticel to compound ray; ×25.

FIG. 12.—Portion of transverse section of *Quercus palustris,* showing relation of transverse lenticel to aggregate ray; ×25.

FIG. 13.—Portion of transverse section of *Alnus rugosa,* indicating close relation between lenticels and aggregate rays; ×27.

FIG. 14.—Portion of transverse section of root of *Sambucus canadensis,* with lenticel on either side of rootlet; ×10.

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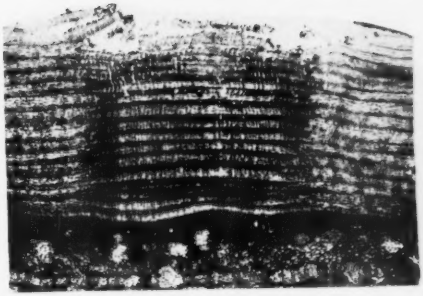

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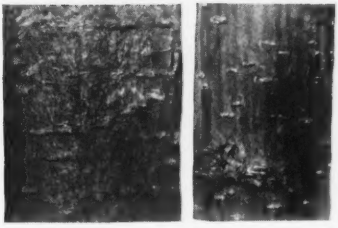

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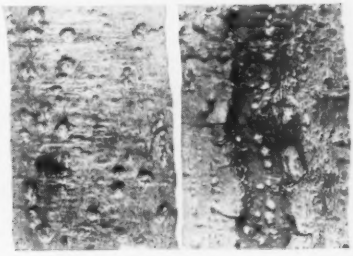

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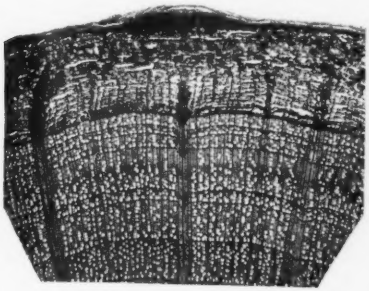
WETMORE on LENTICELS IN DICOTYLEDONS



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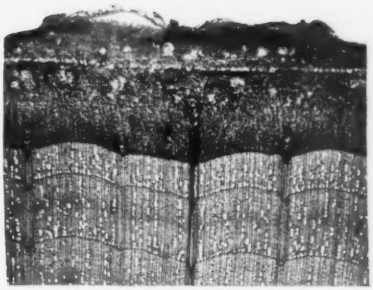

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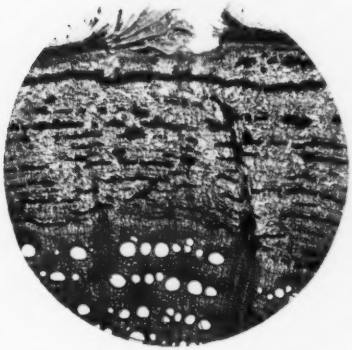

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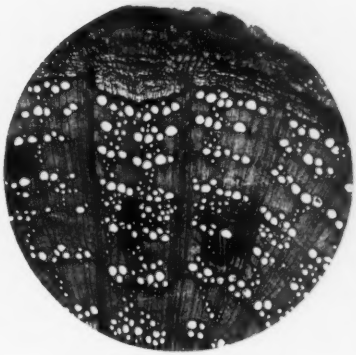

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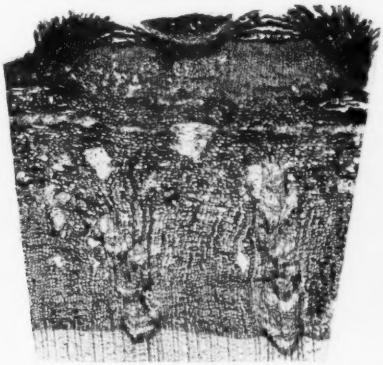

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WETMORE on LENTICELS IN DICOTYLEDONS

ABSORPTION OF WATER BY BARLEY SEEDS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 350

H. S. WOLFE

(WITH ONE FIGURE)

Introduction

The phenomenon of semipermeability of non-living plant membranes seems to have been first observed just twenty years ago by GOLA. Extensive studies of delayed germination (3) apparently led him to the discovery that when seeds were allowed to imbibe water from salt solutions, only the water entered the seed itself; and the existence of a selective semipermeable layer in the seed coat was effectively demonstrated and announced (4). As this latter paper, announcing the discovery of a semipermeable seed coat membrane has hitherto escaped the notice of workers in this field, it may be of interest to note that in an examination of the seeds of 500 species belonging to some forty families, such a membrane was found to be regularly present except in the Leguminosae and in certain genera of the Cistaceae and Cruciferae. In some cases, notably that of the seed of *Cucurbita pepo*, this membrane was removed from the seed coat and used as the septum of an osmometer. GOLA'S thesis was the function of the semipermeable membrane in protecting the seed from being penetrated by toxic solutes while taking in water for germination in the ground, however, and being interested in the ecological phases only, he made no quantitative studies of the rate of water intake from salt solutions through this membrane.

Two years later, BROWN (1) announced what he supposed to be the first discovery of a non-living semipermeable plant membrane, found in barley seeds. He did, however, make the first quantitative study of the phenomenon. Later (2) he amplified his data considerably, and various other workers contributed extended quantitative studies made on other seeds; notably SCHROEDER (7) on wheat, and SHULL (8) on cocklebur. No further studies on barley appeared until

1919, however, when PICKLER (5) published the results of his investigation of the diastatic activity of barley seeds and its relation to their moisture content.

PICKLER found that barley seeds soaked in a saturated solution of LiCl could take therefrom considerable quantities of water. As he is careful to point out, these results are in striking contrast to those obtained by SHULL with cocklebur, the latter demonstrating that there is practically no absorption of water from such a solution. This difference in behavior might be accounted for by the very different nature of the seed coats in the two cases, but that BROWN'S work on barley is as hard to reconcile with PICKLER'S as is SHULL'S work on cocklebur.

BROWN did not use LiCl, but found that from a saturated solution of NaCl, barley grains would take up water, until after 48 hours an equilibrium was reached, when they had absorbed 14 per cent of their air-dry weight, and that after twelve hours they had gained only 10 per cent in weight. On the other hand, PICKLER did not approach nearly to the equilibrium condition, but stopped at the end of twelve hours, when he reported barley grains to have taken up from saturated LiCl solution 27 per cent of their air-dry weight. Now RACIBORSKI (6) gives 375 atomospheres as the osmotic pressure of a saturated NaCl solution at 20° C., and 965 atmospheres for saturated LiCl at the same temperature. PICKLER fails to state at what temperature he saturated his solution, but saturated at the temperature of the experiment (30° C.) its osmotic pressure should have been well over 1000 atmospheres. We have reported here, therefore, a greater intake of water against a resistance of 1000 atmospheres than against 375 atmospheres, and PICKLER'S value agrees fairly well with that obtained by BROWN for absorption from a M-NaCl solution, with only about 40 atmospheres of osmotic pressure.

Despite this great divergence from what all previous work would lead us to expect, there was the possibility that this variety of barley was unique, for BROWN used a hulled barley, *Hordeum vulgare* var. *coerulescens*, while PICKLER employed *H. vulgare* var. *coeleste*, a hullless variety. Although SCHROEDER and BROWN had obtained similar results with wheat and barley respectively, and the latter had shown that the removal of the glumes did not affect the behavior of his

barley, it remained to be proved definitely whether PICKLER's barley followed the rule for all other grains or was in a class by itself. Accordingly, an investigation was made of the behavior of this variety of barley in regard to absorption of water from solutions of salts, especially of LiCl.

Materials and methods

The grain used in these experiments was White Hull-less barley obtained from Vaughan's seed store in Chicago, the same variety and from the same source as that employed by PICKLER in his studies.

All experiments were conducted with media at 30° C., using an electrically controlled thermostat water bath. Saturated solutions of LiCl and NaCl were made up in stock bottles kept in the water bath, with excess of salt in the bottom of the bottles to insure saturation of the solution at the temperature of the experiment. Besides these two solutions only distilled water was used, so that whenever reference is made to LiCl or NaCl, these saturated solutions are to be understood.

The method employed was essentially that first outlined by BROWN. A known weight of grain was soaked for a definite period of time in solutions of known concentration of salts. Then the grains were removed, dried carefully on the surface and weighed, and the increase in weight calculated as percentage of the air-dry weight. A uniform procedure was adopted for this superficial drying, which is to be inferred whenever "drying" is used without qualification. The grains were rolled on dry filter paper for one minute, and then rubbed gently with a soft dry cloth for one minute. Usually twenty-five grains, carefully selected to eliminate injured ones, were employed in each determination, although in a few cases only ten grains were used.

After this superficial drying and weighing, the soaked seeds were then dried to approximately constant weight in a 50° C. vacuum oven. This is an important advance on previous methods, as it gives the actual moisture content of the soaked seeds; and when the original air-dry moisture content is known, it is possible to determine how much of the increase in weight is actually due to water intake.

While samples of grain dried in the oven simultaneously gave closely concordant values for the hygroscopic moisture in the air-dry seeds, samples taken on different days and dried in the oven for much longer periods gave values differing by as much as 1 per cent in a total of 10 per cent. To offset this source of error and to avoid the great length of time necessary for drying to absolutely constant weight (nearly two weeks), a sample of air-dry grain was put in the oven with every series of samples of soaked grain, and the air-dry value so obtained used as the factor for the calculations on the seeds of this series.

Two further refinements of technique were of value. In some cases the grains, after the stated period in the solution, were rinsed for one minute in running water after the first drying and weighing, and then dried and weighed again. In other cases the oven-dried seeds were washed in running water for one hour, and then oven-dried again. These variations in method made it possible to determine whether salts were penetrating the seed coat or remaining superficial only. All percentages recorded in the data are on the basis of air-dry weight.

Experimental results

Increase in weight in LiCl and H_2O

Barley grains were soaked in LiCl and in water for periods of from 30 seconds to 12 hours, then dried and weighed. Table I shows the results of these experiments, and also gives for comparison the data obtained by Pickler for some of the periods employed. The values for absorption from water are not very different in the two sets of data, his being consistently a slightly higher percentage, but the absorption from LiCl is totally dissimilar. Fig. 1 presents these data graphically and more strikingly. The LiCl curve for the data of these experiments flattens out very early, with a maximum at about 7.5 per cent, and has reached only 9 per cent after 200 hours, whereas in Pickler's data the LiCl curve is still rising rapidly at the end of twelve hours, and has already reached 27 per cent. This curve is quite similar to that given by Brown for absorption from M-NaCl.

TABLE I

GAIN IN WEIGHT OF BARLEY SEEDS IN WATER AND IN LiCl SOLUTION FOR PERIODS UP TO 12 HOURS; PICKLER'S FIGURES ALSO GIVEN FOR COMPARISON

TIME OF SOAKING	GAIN IN PERCENTAGE OF AIR-DRY WEIGHT IN		CALCULATED FROM PICKLER'S DATA	
	LiCl	H_2O	GAIN IN PERCENTAGE OF AIR-DRY WEIGHT IN	
			LiCl	H_2O
30 seconds	0.72	3.57		
1 minute	0.79	3.45		
2 minutes	0.81	4.94		
5 minutes	1.61	5.61		
10 minutes	2.38	7.86		
30 minutes	3.50	10.46		
60 minutes	4.90	12.29		
2 hours	5.95	18.57	14.85	21.27
4 hours	6.65	25.67	19.00	29.17
6 hours	6.89	22.65	21.21	34.18
8 hours	6.65	31.35	23.86	38.95
10 hours	7.53	34.44	25.75	43.72
12 hours	7.29	39.33	26.85	46.25

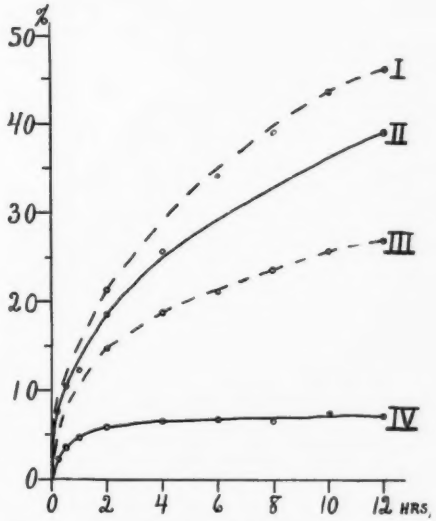

FIG. 1.—Curves showing increase in weight of barley grains in water (I and II) and in LiCl (III and IV); broken line curves from PICKLER'S data; abscissae, time of soaking seeds; ordinates, gain in weight of seeds as percentage of air-dry weight.

Nature of increase in weight

Having determined the amount of increase in weight on soaking in LiCl, the question arose as to whether this were all due to the absorption of water. Preliminary experiments indicated that such was not the case, and further experimentation gave the results summarized in table II. Seeds were soaked, dried and weighed, then oven-dried and weighed; and some were then washed, oven-dried and weighed again. The air-dry factor for the final oven drying was 11 per cent for all except the 200 hour sample, for which it was 11.5 per cent.

These data show that by no means all of the increase of the weight of seeds soaked in LiCl is due to intake of water. The water intake has practically stopped by the end of the second hour, for even after 200 hours the increase in water content was hardly greater than at the end of two hours. The rest of the gain in weight is due to LiCl, which is only superficially absorbed, however, for it can all be removed by an hour's washing in running water. There appears to be a slight increase in absorption of LiCl with time, but as there is only one determination for 200 hours, no very definite statement can be made. The data show a steady increase in LiCl absorption for the first twelve hours, these five samples having been run simultaneously. The next four 12-hour determinations give variable values, however, but all within 0.5 per cent of the mean. It should be stated that variations of less than 1 per cent are not to be considered significant, as this is within the limit of experimental error for the drying of the seeds, and for the variation in different lots of seeds. The figures on which conclusions are based are not only concordant to less than 1 per cent, however, but are themselves of an order much larger than this.

Attention is called to the close correlation between the air-dry moisture content, as determined on several different samples of seeds, and the sum of the amount of loss below air-dry on oven drying plus the amount of gain not accounted for as water. This, of course, simply confirms the values obtained under the conditions of oven drying in these cases for the air-dry moisture content of the samples, but such confirmation is important. Of even greater interest is the correlation between the gain in weight unaccounted for as

TABLE II

ABSORPTION OF WATER AND SALT FROM SATURATED SOLUTIONS OF LiCl BY BARLEY SEEDS

HOURS IN LiCl	WEIGHT (GM.) AIR-DRY	WEIGHT (GM.) SOAKED	WEIGHT (GM.) OVEN-DRY FIRST TIME	WEIGHT (GM.) OVEN-DRY SECOND TIME	PERCENTAGE GAIN IN WEIGHT IN SOLUTION	TOTAL H_2O IN SEEDS SOAKED	TOTAL H_2O IN SEEDS AIR-DRY	PERCENTAGE GAIN IN WEIGHT DUE TO H_2O	PERCENTAGE GAIN IN WEIGHT NOT H_2O	PERCENTAGE LOSS BELOW AIR-DRY ON FIRST DRYING	PERCENTAGE LOSS BELOW AIR-DRY ON SECOND DRYING	SAME CORRECTED FOR AIR-DRY H_2O	PERCENTAGE LOSS IN WEIGHT DUE TO WASHING
1.....	1.0520	1.1035	0.9690	.....	4.90	12.78	10.50	2.30	2.60	7.90	.....	.....	.....
2.....	1.0250	1.0860	0.9425	.....	5.95	14.00	10.50	3.50	2.50	8.00	.....	.....	.....
4.....	1.1580	1.2350	1.0790	.....	6.65	13.50	10.50	3.00	3.65	6.85	.....	.....	.....
10.....	1.0620	1.1415	0.9900	.....	7.53	14.27	10.50	3.75	3.80	6.74	.....	.....	.....
12.....	1.0570	1.1340	0.9880	.....	7.29	13.81	10.50	3.30	4.00	6.52	.....	.....	.....
12.....	1.1205	1.2030	1.0415	0.9965	7.36	14.40	10.50	3.90	3.45	7.05	11.07	10.57	3.52
12.....	1.1495	1.2300	1.0660	1.0160	7.00	14.26	10.50	3.80	3.20	7.26	11.61	11.11	3.85
12.....	1.1750	1.2585	1.0930	1.0455	7.10	14.10	10.50	3.60	3.50	7.00	11.02	10.52	3.52
12.....	1.1830	1.2600	1.0975	1.0470	6.50	13.75	10.50	3.25	3.25	7.23	11.50	11.00	3.77
200.....	2.2645	2.4700	2.1605	1.9900	9.10	13.70	10.00	3.70	5.40	4.59	12.10	10.60	6.00

water, and the loss in weight on washing after the first oven drying. This loss in weight is slightly greater than the theoretical in three of the five cases, probably indicating that there has been some leaching of the salts normally present in the seeds, but the closeness of the correlation amply justifies the conclusion that very little of the loss in weight on washing is to be explained thus.

A modification of this procedure was used at first, and yielded very interesting results, although not definitive. The seeds were soaked in LiCl, dried and weighed, rinsed in running water for 15–60 seconds, and dried and weighed again. The whole process, from taking the seeds out of the solution to the end of the final weighing, occupied less than 10 minutes, so that loss by evaporation was negligible. As there was no oven drying, no data were obtained regarding the absolute amounts of water in the seeds, but it was at once observed that with increase of rinsing time up to 60 seconds, decrease in seed weight followed, despite the fact that seeds were absorbing water rapidly during the rinsing. With periods of rinsing longer than 60 seconds, absorption of water was greater than loss of salt.

In table III are given the results of two sets of experiments of this kind, in which the seeds had been soaked for 12 hours and rinsed for 60 seconds. As a control, to determine the increase in water content due to rinsing, there is used one of the samples from table II which happened to be almost exactly the average for the five 12-hour samples. In the present experiment two samples were washed again after oven drying, and the other two were dried with them a second time without washing, so as to give a correction factor for any greater drying the second time. The factor was 0.6 per cent in both cases, and it is duly subtracted in the proper column.

These data show that nearly all of the absorbed LiCl is rinsed off in 60 seconds when the seeds are still moist. No attempt was made to determine the minimum time for complete removal of absorbed salt, as the only important point was the possibility of completely removing it by fairly brief washing. There is to be noted a startling agreement in the values given for the total absorption of water by the seeds from LiCl. This unusual concordance is largely due to the use of a common factor (14.1 per cent) for determining

TABLE III

EFFECT OF BRIEF RINSING ON WATER AND SALT ABSORPTION

SAMPLE	PERCENTAGE GAIN IN WEIGHT IN SOLUTION a	PERCENTAGE GAIN IN WEIGHT AFTER RINSING b	PERCENTAGE LOSS IN WEIGHT ON RINSING $c=a-b$	TOTAL PERCENTAGE H_2O IN SEEDS SOAKED d	PERCENTAGE INCREASE IN H_2O OVER UNRINSED e	TOTAL PERCENTAGE H_2O IN SEEDS AIR-DRY f	PERCENTAGE GAIN IN WEIGHT DUE TO H_2O $g=d-f$	PERCENTAGE GAIN IN WEIGHT NOT H_2O $h=b-g$	TOTAL PERCENTAGE LOSS BY RINSING $i=c+e$	PERCENTAGE LOSS BELOW AIR-DRY ON FIRST OVEN-DRYING	PERCENTAGE SAME ON SECOND OVEN-DRYING k	PERCENTAGE LAST CORRECTED FOR AIR-DRY H_2O l	PERCENTAGE LOSS IN WEIGHT FROM WASHING $m=l-j$	PERCENTAGE LiCl ABSORBED IN 12 HOURS $n=h+i$	PERCENTAGE H_2O ABSORBED IN 12 HOURS $o=a-n$
1	8.27	7.72	0.55	17.10	3.00	10.50	6.60	1.10	3.55	9.38	11.44	10.84	1.45	4.65	3.60
2	8.21	7.71	0.50	17.00	2.90	10.50	6.50	1.20	3.40	9.27	(9.85)	(0.60)	.....	4.60	3.60
3	7.55	6.96	0.60	16.58	2.50	10.50	6.10	0.85	3.10	9.63	11.43	10.83	1.20	3.95	3.60
4	7.69	6.94	0.75	16.71	2.60	10.50	6.20	0.75	3.35	9.77	(10.35)	(0.60)	.....	4.10	3.60
Control	7.11	.....	.....	14.10	.....	10.50	3.60	3.50	.....	7.00	11.00	10.50	3.50	3.50	3.60

the increase of water in rinsed over unrinsed seeds, as previously explained, but 3.6 per cent is the average figure for the five 12-hour samples of table II, and so undoubtedly is the correct average for the samples of table III, although probably inaccurate for any one of them.

Behavior of water-soaked seeds in LiCl and NaCl

As a final test, grains of barley were soaked in distilled water for 12 hours, dried and weighed, and at once put into saturated LiCl solution containing excess of salt. After 12 hours the grains were removed, dried and weighed again. A second pair of samples was treated similarly, but with NaCl instead of LiCl. Table IV gives the results of these experiments.

TABLE IV

Loss of weight of water-soaked barley grains in LiCl and NaCl

Salt solution used	Air-dry weight of seeds (gm.)	Weight (gm.) after 12 hours in H_2O	Percentage gain in weight	Weight (gm.) after 12 hours in salt	Percentage gain over air-dry	Percentage loss of weight in salt
Saturated LiCl.....	1.1410	1.5790	38.39	1.3365	17.14	21.25
	1.2015	1.6725	39.20	1.4175	17.98	21.22
Saturated NaCl.....	1.0555	1.4649	38.79	1.2910	22.31	16.48
	1.2570	1.7625	40.57	1.5510	23.40	17.17

Of course the seeds were far from being in equilibrium with the solution at the end of 12 hours, but in LiCl the water content has dropped from an initial 39 per cent to below 18 per cent, and in NaCl to below 23 per cent. This takes no account of the amount of this gain over air-dry weight which is due to salt absorption, and as the previous data have shown this to be about 4 per cent for LiCl, it is seen that the water content has really dropped to near 14 per cent. Experiments not here reported have shown that after 12 hours in NaCl, barley grains have increased about 11 per cent over their air-dry weight, and there seems little reason to doubt that with longer periods of time an equilibrium would be reached under these conditions at about 8 per cent for seeds in LiCl and 11 per cent for seeds in NaCl. The point of importance, however, is the impossibility of barley grains increasing to 27 per cent over their air-dry weight by

absorption of water from saturated LiCl solution, as PICKLER reported, or even from saturated NaCl in 12 hours; for when put into these solutions with a greater water content than this, they lost within 12 hours until they had only half as much water in them in the LiCl sample, and considerably less than 27 per cent in the NaCl sample.

Discussion

The results of the present investigation are so different from those obtained by PICKLER that comparison is almost impossible. There seems to be no possible explanation of this unconformity other than that he used by mistake some other salt instead of LiCl (although this is almost unthinkable). The absorption curve of his data is unmistakably that for a solution of low osmotic pressure, and his germination studies indicate that his seeds really absorbed from solution considerable quantities of water.

It was thought at first that his anomalous results might be due to employment of a solution saturated below the temperature of the experiment, but experiments conducted under such conditions showed only insignificantly greater increases in weight of seeds. Also the very form of the absorption curve precludes the possibility of the solution having been nearly saturated. It is unfortunate that PICKLER did not try cocklebur seeds when he found barley exhibiting such different behavior, for he certainly would have found a large intake of water from his solutions by cockleburs also.

The present study leaves no doubt that air-dry barley grains are not able to exert such tremendous internal imbibitional force as would be indicated by PICKLER'S observation of 27 per cent intake of water in 12 hours from LiCl against an osmotic pressure of 1000 atmospheres. The seeds, however, are able to take in about 3.6 per cent of water from such a solution in 12 hours at 30° C., whereas SHULL reported no absorption by cocklebur seeds under the same conditions, except that he used room temperature which would affect only the rate at which equilibrium was attained, so far as we are concerned. This lack of conformity may mean that barley seeds have a greater imbibitional force when air-dry than have cocklebur seeds, but the structure of the seed coats must be taken into consideration.

A median section of the cocklebur seed shows that it consists of an outer epidermal layer, a middle stratum of four or five layers, and the inner layer representing the nucellar epidermis. This last is the semipermeable layer proper, as SHULL demonstrated, but the middle layers are greatly compressed and have some osmotic properties. The outer layer represents nearly half the thickness of the entire seed coat, and is quite chaffy and fragile. There is no doubt that in his efforts to remove all surplus water and salt, SHULL rubbed off this outer layer in the process of drying the seeds. There would be left very little of the seed coat outside of the semipermeable layer to hold water, and if the membrane were truly semipermeable to LiCl, and that salt in saturated solution equaled or exceeded the internal attractive forces of the seed, then no increase in weight would be observed.

Barley grains, on the other hand, are well known to be not seeds at all, but fruits with pericarps of firm texture. In the case of the hull-less variety used in these experiments, there are about ten layers of cells external to the semipermeable layer, which both GOLA and BROWN showed independently to be the single remaining layer of the nucellus, its epidermis. The degree of rubbing which would remove the outer layer of the cocklebur seed coat would hardly affect that of the barley, and its seed coat is shown by microscopic measurement to have three times the thickness of the portion of the cocklebur seed coat left after the outer layer has been rubbed off. The quantity of water which these external layers of the barley coat can hold is manifestly not at all negligible. Furthermore, the barley grain has a deep longitudinal suture, which holds water very tenaciously even with careful drying, while the cocklebur seed is quite smooth of surface. It is therefore entirely reasonable that barley grains should show greater increase in weight than cocklebur seeds, in solutions of the same osmotic pressure, and such greater gain does not necessarily indicate a greater internal attractive force for water by barley.

The most important point which this study brings out is that gain in weight in solution is not an indication that seeds are withdrawing water from the solution. Previous investigators seem to have overlooked the possibility of salt absorption, and have assumed that all gain in weight was due to intake of water. As a matter of

fact, neither BROWN nor PICKLER had any data on the amount of water imbibed, but only as to the combined absorption of water and salt. Whereas in the cockelbur seeds there was no absorption of either water or salt, for reasons already given, in the barley grains considerable salt can be held by the many layers external to the nucellus. A saturated solution of LiCl is very viscous, and clings closely to the surface of the barley grains, as well as accumulating in the suture.

From the fact that there seems to be no increase in the water absorption after the second hour, while the salt absorption seems to increase slowly though steadily with time, the conclusion may be drawn that there is a precipitation of the salt in these superficial layers of cells where the salt and water are absorbed. The data are very meager for determining this point, but in substantiation may be cited that after 12 hours in LiCl a greater weight of salt has been absorbed than of water, although in a given volume of the solution there is a greater weight of water than of salt, 85 per cent being the weight solubility of LiCl at 30° C. The ease with which the salt can all be washed out is strong proof that it is really all located in these superficial layers external to the semipermeable one, and, furthermore, if salt penetrated deeper, then water would be taken in deeper also, whereas the data show that water absorption quickly reaches a maximum and remains constant thereafter.

When barley grains which had been soaked for 12 hours in LiCl were cut open, their endosperm was found to be quite dry still. Even after 200 hours' soaking this was true. Also, after 12 hours' soaking in LiCl the grains still retained their original pearly luster, whereas 10 minutes in water was sufficient to cause the loss of this, the acquisition of a certain translucence in its stead, and a softening of the endosperm. This opacity of aspect seems to be lost as soon as the endosperm begins to take in water. All these considerations make it seem evident that barley grains are not able to extract water through their semipermeable membranes against the resistance offered by saturated solutions of LiCl, although the layers external to this membrane may absorb considerable quantities of water and of salt.

It is interesting to note that BROWN found that barley grains could not absorb enough water from 36 per cent H_2SO_4 to moisten

the endosperm perceptibly. Although still as brittle as ever and apparently air-dry, yet there is probably some slight increase in moisture content, since SHULL (9) found in other seeds of the same family that when they were exposed over 36 per cent H_2SO_4, there was a gain of about 3 per cent in weight. The boiling point of such acid is about 115° and its freezing point −63° C. Calculations of the osmotic pressure from these colligative properties of the vapor pressure agree at about 650 atmospheres. We have, therefore, no intake of water against 1000 atmospheres pressure, not enough to cause any apparent change in endosperm texture or appearance against 650 atmospheres, but quite appreciable intake, with evident endosperm moistening, against the 375 atmospheres of NaCl.

Summary

1. Barley grains which have been soaked in saturated solutions of LiCl for periods of from 30 seconds up to 12 hours show a curve of increase in weight which has practically reached its maximum of 7.5 per cent at the end of the first 2 hours.

2. When such grains, after 12 hours' soaking, are oven-dried, they fail by 3–5 per cent to lose weight equivalent to their gain in weight plus their original air-dry content of moisture, that is, they have either absorbed or adsorbed some salt.

3. When these oven-dried grains are washed for an hour in running water and are then oven-dried again, they show a loss in weight of about 3–5 per cent over the first oven-dry weight, that is, the salt is so located that it is readily washed off.

4. Grains which after 12 hours in LiCl are rinsed for 60 seconds in running water before oven-drying, fail by only 0.5–1.0 per cent to dry to the theoretical oven-dry weight, and on further washing for an hour lose about that much more weight.

5. The average of eight determinations gives 3.6 per cent of water absorbed in 12 hours from saturated LiCl at 30° C., the rest of the observed weight being due to absorbed salt.

6. More water is absorbed by barley grains from distilled water in 2 minutes than from LiCl in 12 hours, and there is more gain in weight in 12 minutes in distilled water than in 12 hours in LiCl.

7. The increase in weight of barley grains soaked in LiCl is due to absorption of water and salt by the numerous layers of the grain

external to the semipermeable layer, and not to penetration of either water or salt into the interior of the grain.

8. The data obtained in these experiments agree quite well with those obtained by BROWN, SCHROEDER, and SHULL with other seeds, but show no agreement with those given by PICKLER for the same variety as was here used. No explanation seems possible for this unconformity, except that perhaps PICKLER did not use LiCl as he supposed he did, and such an explanation is hardly entertainable.

9. Attention is called to the error commonly made of assuming that the increase in weight of seeds placed in salt solutions, especially saturated solutions of great viscosity, is due entirely to intake of water. Actually it may be that as much as half of this gain in weight is due to absorbed salt.

It is a pleasure to express my obligation to Professor CHARLES A. SHULL, who first called my attention to the anomalous findings which suggested this study, and who has been of assistance throughout the investigation.

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BRIEFER ARTICLES

CORRUGATED ALUMINUM SHEETS FOR THE BOTANIST'S PRESS

(WITH TWO FIGURES)

For several years past corrugated pasteboards between the felt driers in the plant press, together with the use of artificial heat, usually from a kerosene stove or camp fire, have proved a great boon to the collecting botanist, especially when sunshine is rare and rain constant. Such devices have been admirably described by HITCHCOCK,[1] and little can be added to his discussion. I have used equipment much like that of HITCHCOCK'S with great satisfaction, being able to dry a day's collection over night, even though the plants were wet with rain and the driers also soaked. The corrugated pasteboards are bulky and comparatively heavy, however, and I therefore venture to describe the following lighter and more compact press equipment.

Instead of the corrugated pasteboard, aluminum sheets cut 30.5×61 cm. and 0.15 mm. thick are corrugated by running grooves 4 mm. deep and 13 mm. wide across them. The result, after corrugating is completed, is a sheet 30.5×38 cm., approximately the dimension of the usual drier.

Specimens are placed as usual in folders of newspaper or other similar paper. The folders may then be placed between two ordinary driers and these between two sheets of corrugated aluminum. Thus the normal sequence is drier, folder, drier, aluminum. The thinnest botanical drier that gives sufficient stability is best.

In practice I find that often half the number of driers just suggested can be omitted, and that three folders can be placed between two aluminum sheets, making the sequence drier, 3 folders, aluminum. Whether the specimen next to the aluminum will show any corrugation or not depends upon its nature. Often there is no apparent effect, and almost always it is very slight. If the kind of specimens permit it all the driers may be omitted, therefore, only the folders and aluminum sheets being used. Familiarity with the nature of the plants collected will readily enable the collector to decide whether, and to what extent, felt driers are necessary. The gain by decreasing the size of the pack enables the handling of more

[1] HITCHCOCK, A. S., Jour. N.Y. Bot. Gard. **21**: 129–137. 1920. ———, Methods of descriptive systematic botany. 1925.

than three times as many folders. The aluminum, doubtless due to its capacity to conduct heat, results in much more rapid drying than by the use of corrugated pasteboards.

Instead of the usual wire frames for each side of the pack, aluminum frames can be used, with a great saving of weight. Such aluminum cast frames are shown in fig. 1. These measure 30.5×46 cm., and 6 mm. in section.

To support the press over the heater, a table made by screwing aluminum legs into the four corners of a press side, constructed with special

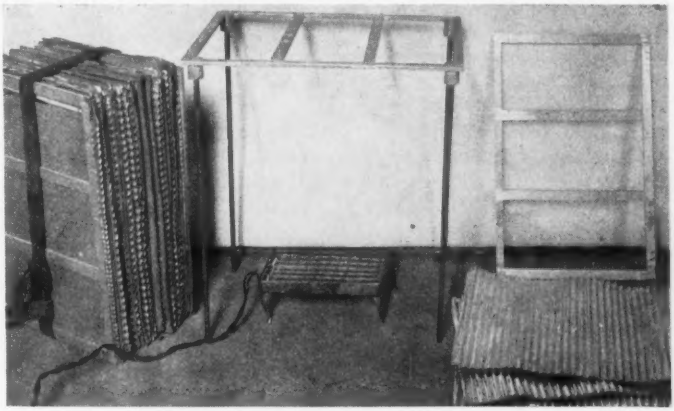

FIG. 1.—Press equipment: pack made up ready for drying, aluminum table with iron legs, electric heater, aluminum press ends, and three corrugated aluminum driers.

corners to receive the legs, is an improvement on temporary camp supports. Two lengths of legs should be carried, one set 30 cm. long to use with electrical heat, such as the electric toaster shown in fig. 1, and one set 48 cm. long to use over a kerosene heater. To secure the necessary pressure on the pack, a trunk strap of suitable length is best.

Electricity is the most useful heat, and is now available so generally that provision for its use should be made. An electric toaster with removable legs packs with economy of space.

Kerosene may be used when electricity is not available, employing a small two-wick stove. Still better perhaps is the plan of having made two kerosene reservoirs (fig. 2), about 29×6 cm., and fitting each with a burner taken from an ordinary kerosene stove. These pack economically and give a large kerosene capacity. In some instances it may be ad-

visable to substitute canned heat for kerosene, but I cannot yet speak from experience regarding its use.

The pack when made up is placed upon the table with the corrugations in a vertical position. A skirt of khaki is then placed around the pack, its bottom reaching to the floor, its top sufficiently secured in place

FIG. 2.—Drier set up over kerosene stove with specially constructed reservoir

by tucking the edge in the pack. A second pack also with a skirt may be placed on top of the first (fig. 2). The plants in this second pack will be considerably dried, although of course not so thoroughly as those in the lower pack.

The convenience of the outfit is such that it can be set up in less than five minutes and packed away for transport in a similar time.—F. L. STEVENS, *University of Illinois, Urbana, Ill.*

CURRENT LITERATURE

BOOK REVIEWS

Revaluation of biological concepts

The relativity and quantum theories have necessitated the revaluation by scientists and philosophers of the data and concepts of the physical sciences. Naturally the biological sciences could not very long escape a similar revaluation. Because of the prestige of the physical sciences, biology "apes the manner of physics" and it has been "orthodox to hold that there is nothing in biology but what is physical mechanism under somewhat complex circumstances." Consequently a revaluation of the data and concepts of the biological sciences is due, not only because revaluation is in the air, but even more because the philosophical foundations on which biology builded its concepts are giving way. This situation is very ably and clearly discussed by WHITEHEAD[1] in *Science and the modern world*, from which the quotations are taken. WHITEHEAD further states: "It cannot be too clearly understood that the various physical laws which appear to apply to the behavior of atoms are not mutually consistent as at present formulated. The appeal to mechanism on behalf of biology was in its origin an appeal to the well-attested self-consistent physical concepts as expressing the basis of all natural phenomena. But at present there is no such system of concepts." WHITEHEAD also criticizes the current vitalisms for accepting mechanism based on materialism and merely introducing an additional vital factor. He contends that science is taking on a new aspect which is neither purely physical nor purely biological; it is becoming the study of organisms. Biologists will find this an interesting and stimulating book in spite of its heavy flavoring with metaphysics.

ELDRIDGE[2] subjects the data of biology to a logical, philosophical, and metaphysical analysis. Such problems as inheritance of acquired characters, variation, and heredity receive exhaustive and critical treatment. The author contends that the phenomena of organization and regulation as we see them in organisms defy attempts to fit them into the concepts of materialistic mechanism which have dominated the philosophy of science. The author in the light of logic and philosophy prefers to choose the path of the vitalists. The vitalistic conceptions of BERGSON, DRIESCH, and others, however, are subjected to the same critical analysis applied to the mechanistic conceptions. The author's vitalism

[1] WHITEHEAD, A. N., Science and the modern world (Lowell Lectures 1925). Pp. xi+296. Macmillan Co. 1925.

[2] ELDRIDGE, SEBA, The organization of life. pp. xv+470. Thomas Y. Crowell Co. 1925.

is one which permits functional activity and experience to affect the "organizatory factors." Although the entelechies advocated can apparently be of little aid at present to the experimental biologist, he should not let this fact prejudice him against the book. Its value lies in its critical analysis of the data and concepts of biology. ELDRIDGE's book carries an introduction by H. S. JENNINGS which is a thorough-going and fair review. The following quotations are taken from the introduction. "The author has surveyed the chief doctrines of vitalism, mechanism and their congeners, with the arguments offered for and against them, and sets these forth clearly. He prepares for us a map of this wilderness, marking the paths leading to different destinations; and putting up at each fork a sign calling attention to the different fates in store for us according as we take the path to the right or that to the left. . . . . The map maker gives us . . . . his own preferred route. . . . . His conclusions lie in the opposite direction from those reached by the present writer over *his* preferred path of radically experimental analysis. For the serious student, intending to determine his own route, the map is more important than the recommendation as to preferable roads." "The work, too, is a concrete example under the conviction that . . . . in addition to observation and experiment, science has a need of far reaching inferential ratiocination for its proper working out. . . . . Beside its use as a compendium of the matters to be weighed and considered in theoretical biology, it gives opportunity for judging the fruits of such extensive ratiocinative treatment of scientific data."—G. K. K. LINK.

Chemical action of ultraviolet rays

Ultraviolet radiations have been found capable of producing many different kinds of chemical reactions, some of which are of unusual interest to the physiologist and physiological chemist. A very extensive literature has grown up, in physical, chemical, and electrical journals, as well as in medical and biological publications. ELLIS and WELLS[3] have summarized the information about ultraviolet rays in book form. The first four chapters may be considered introductory. They deal with the nature of ultraviolet, sources of the rays, the various metal vapor lamps used in artificial production of these rays, and the protective screens, filters, and glasses useful to the investigator. The six succeeding chapters deal primarily with the chemical effects of ultraviolet, the photochemical mechanism, behavior of gases in presence of ultraviolet radiations, photochemical and photolytic reactions, and the influence of these short rays in halogenation reactions. The next four chapters take up the biological reactions, photosynthesis, sterilization by ultraviolet, biological effects on proteins, enzymes, antibodies, chemistry and histology of blood, metabolism, avitaminosis, etc., and therapeutic applications. The final chapter deals with miscellaneous applications of ultraviolet rays, particularly in the industries.

[3] ELLIS, C., and WELLS, A. A., The chemical action of ultraviolet rays. 8vo. pp. 362. *figs.* 85. New York: Chemical Catalog Co. 1925.

Plant physiologists will be most interested in the discussion of photosynthesis, photochemical reactions, sterilization, and biological effects. At the close of the last mentioned chapter, there is a very brief summary of the influence of ultraviolet radiations on germination of seeds and the growth of plants by POPP, who is engaged in extensive investigations of this subject.

The reviewer feels that the authors have possibly not been sufficiently critical toward the interpretations which some investigators have placed upon their work. In some cases where the original sources are hypothetical and speculative to a high degree, these authors give the impression that their claims are practically proved. One must therefore read carefully, and with some reference to the original sources, if he would avoid misjudging the present condition of our knowledge with reference to the effects of light upon chemical metabolism, particularly synthesis, in plants.

The subject had grown to the point where such a book was needed, and it will find a welcome among those who are interested in experimentation with radiations beyond the range of visibility.—C. A. SHULL.

Physiological basis of drought-resistance

The physiological side of drought-resistance has received critical consideration by MAXIMOW,[4] who has drawn together many interesting observations on absorption, transpiration, and the problems of water balance and water deficit in the plant. Unfortunately it is published in Russian, but it includes a brief abstract of about 15 pages in English at the close of the discussion.

The book is divided into three main sections, the first of which consists of four chapters dealing with the absorption of water, the laws governing intake, and the conditions under which water enters the plant. The first chapter considers the suction power idea of URSPRUNG, the influence of water deficit on the growth of cells, anatomical details for reduction of transpiration, and the necessity of the transpiration stream. In chapter II, the author accepts the idea of active and passive absorption, the latter brought about by transmission of suction power developed in the leaves to the root cells through the cohesion of water in the tracheae. The third chapter takes up the soil conditions, its water retaining power, wilting coefficients, and water transporting power. The last chapter of this section deals with the influences of environment, low temperature, bog xerophytism, etc.

The second section, of six chapters, deals with water elimination in liquid and gaseous form, physics of transpiration, stomatal movements, stomatal control of transpiration, and physics of the transpiration stream.

The last half of the book considers the water balance, in five chapters. The normal water balance and conditions causing deficit are considered in chapter XI, while the following chapter takes up the peculiarities of groups of plants

[4] MAXIMOW, N. A., The physiological basis of drought-resistance of plants. 8vo. pp. 436. *figs. 61*. Inst. Applied Bot. and Plant Breeding. Leningrad. 1926.

that differ in water relations, succulents, desert ephemeres, and ordinary xerophytes. Chapter XIII considers the relations between drought resistance and certain physiological and anatomical peculiarities of plants. Little correlation is found between drought resistance and intensity of transpiration, or between transpiration and dry weight production. Chapter XIV examines the problems of xeromorphy from new points of view. The fundamental trait of xeromorphy is said to be "increased density of nervation, which points to an augmented water supply, and an increased amount of stomata pointing to a high transpiration." Xeromorphic plants are not characterized by restricted water relations, but by plastic ones. They possess the capacity to endure extreme wilting without injury, and to carry on more intense vital functioning in times of water abundance.

The final chapter applies the new conceptions of xeromorphy to the problems of breeding drought-resistant plants. Endurance is conditioned mainly by protoplasmic behavior and the accumulation of substances which protect the protoplasm from coagulation under wilting.

MAXIMOW writes that an attempt to have his work translated into English is being made. It is hoped that this may be accomplished, as the work constitutes a stimulating summary of this important physiological agricultural problem.—C. A. SHULL.

The phylogenetic method in taxonomy

HALL and CLEMENTS[5] have published a paper suggesting some fundamental changes in the preparation of taxonomic monographs. The new method is illustrated by monographs of the North American species of *Artemisia*, *Chrysothamnus*, and *Atriplex*. Instead of merely grouping the species on the basis of resemblances and differences, the attempt is made to work out the course of evolution they represent. The results are presented in diagrams, indicating not only the general direction of evolution, but also the characters that have undergone change. Some of the conclusions are as follows.

Artemisia is supposed to have developed from an ancestor resembling *Chrysanthemum* and *Tanacetum*, the most primitive section being *Abrotanum*. *Chrysothamnus* is thought to have developed from a hypothetical group close to a section of *Haplopappus*. In *Atriplex* the probable primitive condition is described, the species most nearly representing it being *A. hortensis*. The authors have drawn their conclusions not only from the ordinary taxonomic characters of these genera, but also from their ecological relationships, as obtained from extensive field work. They urge the inadequacy of herbarium studies unaccompanied by investigations in the field.

The troublesome question of nomenclature is also considered, and the attitude of the authors may be inferred from the following quotation: "There has

[5] HALL, H. M., and CLEMENTS, F. E., The phylogenetic method in taxonomy. Publ. Carnegie Inst. no. 326. pp. 355. *pls.* 58. 1923.

been no hesitation in selecting names from those valid under the American Code when these are preferable, and no compunction has been felt in using names sanctioned by neither code when this has been found to be in the interests of usefulness." This of course is carrying nomenclature back to the days preceding any code and destroying its stability.

Another view advanced relates to the limitations of genera and species. Data are given showing the rapid increase in the number of recognized species during the last few years, and also in the number of recognized genera. HALL and CLEMENTS advocate a return to the old concepts of genera and species, and a checking of the present tendency to extreme segregation. They illustrate this point by contrasting their treatment of *Artemisia* and *Atriplex* with that of the *North American flora*. They accept 29 species of *Artemisia*, while in the other publication these are presented as 125 species in 4 genera. In *Atriplex* they recognize 47 species, while in the other publication these are presented as 106 species in 2 genera. Much of this difference is doubtless due to the emphasis which HALL and CLEMENTS place upon the effect of environmental conditions. These different opinions as to generic and specific limitations can only be reconciled by field study and breeding experiments. Of course the species concept must be considered also, HALL and CLEMENTS urging a return to the larger concept of the older taxonomy.—J. M. C.

Families of flowering plants

Revisions of systems of classification are constantly appearing, and often attract little attention beyond the limits of the small groups immediately favorable or decidedly opposed to the changes they advocate. It seems safe to predict, however, that the present volume[6] will be more widely noticed and will stimulate more interest in the possible relationships between families of angiosperms. It is certainly the most noteworthy attempt to solve the puzzle of phylogenetic lines that has been attempted since the system connected with the names of ENGLER and PRANTL appeared.

Those who regarded the treatment of the Amentiferae and that of the monocotyledons as presented by ENGLER and PRANTL as far from satisfactory, may be pleased with the position given these groups in this new system. HUTCHINSON has ventured to develop double phylogenetic lines, with many branches, having the Ranales and the Magnoliaceae as their respective starting points. From the former has come an herbaceous complex which includes the monocotyledons and many of the families usually placed in the phylum sprung from the Ranunculaceae and culminating in the Asterales (Compositae), Campanales and Lamiales (Labiatae).

From the latter has come a complex that includes the greater number of

[6] HUTCHINSON, J., The families of flowering plants. I. Dicotyledons. Arranged according to a new system based on their probable phylogeny. 8vo. pp. xiv+328. *figs. 264.* London: Macmillan & Co. 1926.

the more strictly arboreal families. This gives emphasis to the fact that trees and shrubs are at least as primitive as herbs. In both groups petaliferous flowers are regarded as preceding apetalous ones, and bisexual as preceding unisexual flowers. This has resulted in giving the Amentiferae a position as a lateral branch decidedly more specialized than the Magnoliaceae from which they are descended through the Rosales.

The proposed system will decidedly increase the number of plant families. Thus while ENGLER and PRANTL in their *Pflanzenfamilien* have some 280 families of flowering plants, including gymnosperms, HUTCHINSON, in this his first volume, makes the dicotyledons include 264 families. He claims that not only are these families composed of more homogeneous material, but also that they are grouped into smaller orders that show closer general relationships. In this grouping resemblances are emphasized rather than differences.

Among some of the features of this volume that should recommend it to the general botanist, if not to the taxonomist, are its introductory discussion of the principles of classification, its key to the families of dicotyledons, its numerous sketch maps showing the distribution of different genera and families, and the originality evident in the drawings illustrating the structure of the flowers of the various families.

The volume is dedicated to the memory of GEORGE BENTHAM and JOSEPH DALTON HOOKER, authors of the *Genera Plantarum*, whose views have influenced the present author in his phylogenetic arrangement.

The printers have done their work well and the volume is certain to stimulate thought, whether the reader is in accord with its theories or not.—GEO. D. FULLER.

Methods of analysis

A revision of the *Official and tentative methods of analysis of the association of official agricultural chemists*[7] is ready for distribution. This standard work will be needed by every physiological chemist and analyst. It is published as a second edition, although the volume issued in 1921 was also called a second edition. The revision brings the results of five years of improvement of methods (1919–1923) into more accessible form. The method of cross reference has been changed to give the page, rather than the chapter and section number. Two chapters are added, one on liming materials, and the other on gelatin. There are some changes in arrangement of chapters, Soils now appearing immediately after Fertilizers; and the chapters on Foods and Feeding Stuffs, and Saccharine Products, are now merged in a chapter on Sugars and Sugar Products. Other minor changes will be noted. There are over 100 additional pages in the revised volume. It is a most useful compendium, and fills a need for authoritative information on the best methods for technical analysis.—C. A. SHULL.

[7] Official and tentative methods of analysis of the Association of Official Agricultural Chemists. 8vo. pp. xvi+535. Published by the Association, Washington, D.C. 1925.

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